

LAND SNAIL DIVERSITY OF THE SAVANNA/FOREST MOSAIC IN LOPE NATIONAL PARK, GABON

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ABSTRACT

We present the assessment of the land snail diversity in approximately 50 km² of savanna/forest mosaic in the northern part of Lopé National Park, Gabon, taking into account habitat variation and seasons. A total of 3,745 specimens were collected, yielding 74 species from 12 families, with Subulinidae being the most speciose family. Most specimens were not identified but assigned to Recognizable Taxonomic Units. Extrapolations suggest that the true diversity of the area lies between 79 and 132 species. Overall snail abundance was low, and most species were minute. Spatial and habitat heterogeneity was high, with 33.8% of the species collected from one station only. Rare species made up a considerable proportion of the fauna, with 23.0% of the species represented by one specimen only. The most species-rich habitats were mature forest, Marantaceae forest, rocky forest, and forest fragments isolated in savanna, in that order. Savanna was the least species-rich habitat, and no species were confined to this habitat. Benefits and drawbacks of the Recognizable Taxonomic Units approach are discussed, and suggestions for maximizing mollusc inventories in tropical forests are proposed.

Key words: Gabon, Mollusca, land-snail, biodiversity, Recognizable Taxonomic Unit, rainforest, rarity.

INTRODUCTION

Tropical rain forests are disappearing or being degraded at an alarming rate all over the world, and African forests have been reduced to one third of their original extent (Sayer et al., 1992). West Central Africa has the largest remaining block of forest, and Gabon retains the highest percentage of forest cover (between 87% and 96% depending on the estimates). However, these forests are now targets for logging companies, and the annual rate of deforestation for Central Africa is 0.6% (Sayer et al., 1992). In Gabon, 68% of the original extent of frontier forests (large, ecologically intact and relatively undisturbed natural forests; Bryant et al., 1997) has been lost, 100% of the remainder is threatened, and the frontier forest index is 68, on a scale from 0 to 99, 99 being the worst possible score (Bryant et al., 1997). Large tracts of forest have dis-

appeared before information on their ecology and biodiversity could be obtained. For sound and reliable conservation actions to be undertaken, it is important to document the diversity within the remaining forests.

In contrast to insect diversity, the mollusc fauna of tropical forests was until recently believed to be relatively depauperate (Solem, 1984). Indeed, the lack of calcium in the soils of the Congo-Zaire and Amazon basins argues against expectations of a rich and diverse malacofauna. Recent studies (Emberton et al., 1996; Tattersfield, 1996; De Winter & Gittenberger, 1998; Gargominy & Ripken, 1998; Schilthuizen & Rutjes, 2001; Seddon et al., 2005) used intensive sampling methods, including litter sieving, and have shown that previous assumptions, at least in part, were wrong: for example, in Cameroon, 97 gastropod species were found in 1 km² of apparently homogeneous forest (De Winter & Gitten-

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berger, 1998); in French Guiana, up to 19 land snail species were found in only 1 m² of forest floor (Gargominy & Ripken, 1998). As most of the species are minute, rare, or hard to find (in these studies, fewer than five individuals were found for many species), the level of diversity is hard to detect. From the little information available (Rogers & Homewood, 1982; De Winter, 1995), it seems that at least some species have a restricted geographical range, which is important from a conservation perspective. Solem (1984) predicted a median range of less than 100 km for all land snail species, and probably less than 50 km, but on the other hand gave a median range of 0.825 km² for 28 species of camaenid land snails in the Kimberley Range (Western Australia) (Solem, 1988a)! His preliminary speculations on generally small range size and high allopatric diversity have been confirmed by subsequent works (reviewed in Seddon et al., 2005).

The general paucity of studies concerning tropical malacofaunas is partly because taxonomists, for whom conservation is not always the first priority, are often reluctant to publish the results of a study before their material is fully identified/described. The lack of taxonomic expertise on molluscs represents a bottleneck (the taxonomic impediment, see the website of the Global Taxonomy Initiative at <http://www.biodiv.org/programmes/cross-cutting/taxonomy/>), emphasized by the fact that there are few comprehensive collections in museums, and that published knowledge is scattered and very limited especially in regard to more recent literature. Notably, there are no checklists for West and Central Africa, and very few for East Africa (Verdcourt, 1983; Bruggen, 1993). As a result, tropical mollusc faunas are poorly known: for instance, there is only a single recent paper (De Winter, 1995) for Gabon, the situation being similar for Congo, Cameroon, and Equatorial Guinea. The main reference we used for identifications during our study dates from 1919 and concerns the Democratic Republic of Congo (Pilsbry, 1919). For West and West-Central Africa, there are altogether approximately 500 papers on molluscs (De Winter, pers. comm.). The contrast with the situation in European countries is striking: for example, Falkner et al. (2002) present a list of 377 references published between 1990 and 1999 dealing with the systematics and distribution of the malacofauna of France alone, besides those

on anatomy or biology; for the same period, the Zoological Record online lists only 15 papers on these topics for Gabon, Cameroon, Equatorial Guinea, and Congo combined.

The northern part of the Lopé National Park is an area of forest-savanna mosaic with a relatively high diversity in the studied groups: for example, approximately 1,400 plant species (White & Abernethy, 1997) and 399 species of birds (Christy, pers. comm.) have been recorded in the area. This high diversity is linked to the high diversity in habitats, from open grassland to dense forest, resulting from the recolonisation of savannas by forest since 1500 B.P., and the impact of human-induced fires in savannas (detailed by White, 2000). The area has had protected status since 1946 and was upgraded from Faunal Reserve to National Park in 2002. Field research has been on-going since 1983, primarily on primates, but also in other areas, including vegetation history, archaeology, and large mammal populations.

The present paper is the result of a conservation-oriented study of the land snail fauna of central Gabon. We document here the molluscan diversity of the northern part of the Lopé National Park and examine its relationship to habitat variation; a separate paper will compare the faunas inside and outside the park (Fontaine et al., in press).

METHODS

Geographical Setting

The study site is the north-eastern part of the Lopé National Park in central Gabon (Fig. 1). Most of the park is covered by semi-deciduous lowland tropical rainforest, with approximately 300 km² of savanna and forest-savanna mosaic along the northern and part of the eastern limits of the park. In our study area, the forest was selectively logged at low intensity (1–2 trees.ha⁻¹) more than 30 years ago, mostly for okoume *Aucoumea klaineana* (Burseraceae) (White et al., 1995). Two major rivers, the Ogooué and the Offoué, as well as many tributaries, run through the area.

The climate is characterised by a well-defined dry season of about three months between June and September, but its beginning and duration vary among years. There is usually a less pronounced and short dry season in January–February. The mean annual rainfall is 1,548 mm, and temperatures vary little

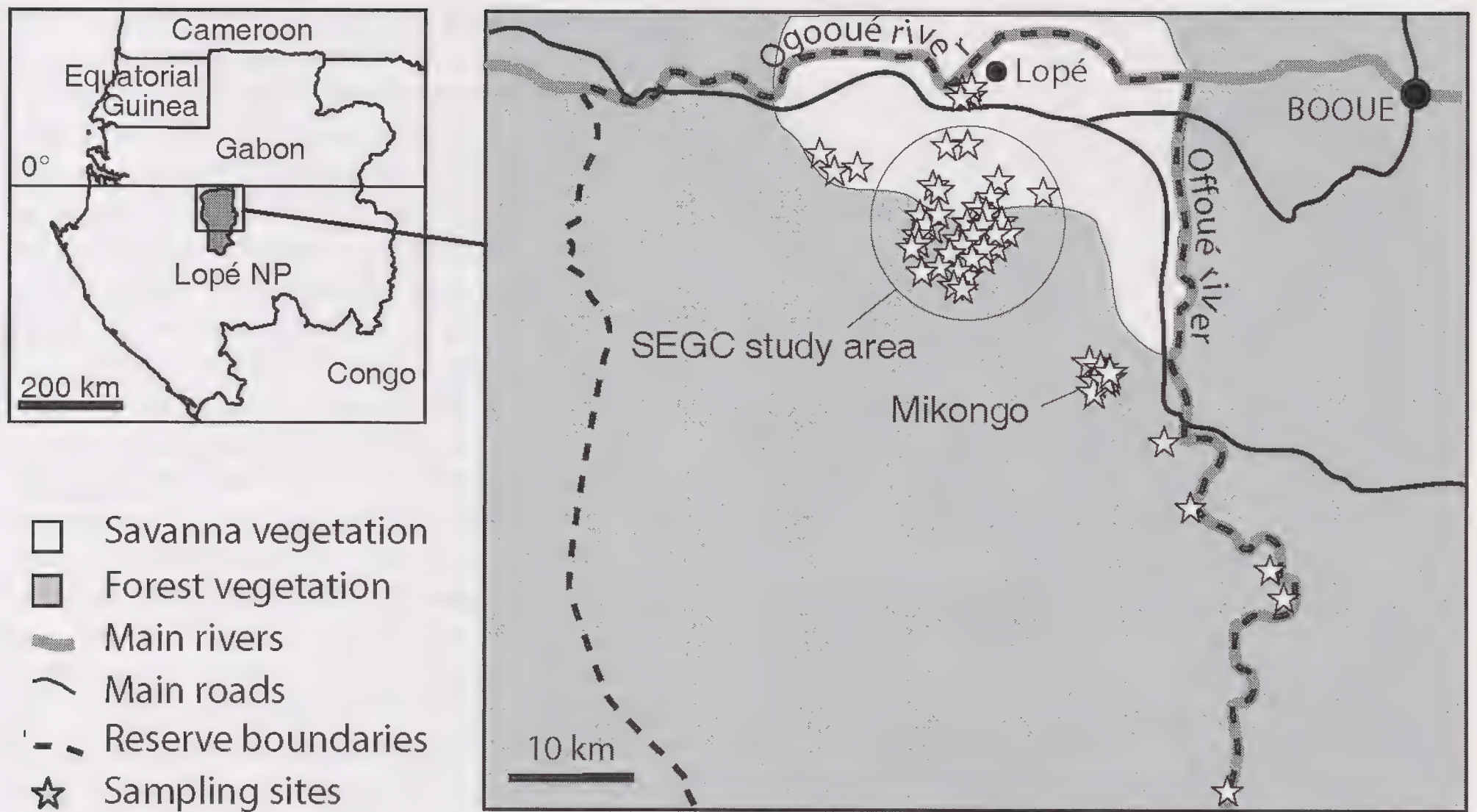


FIG. 1. Location of the study site in Central Gabon, and sampling area of this study.

but are lowest in the dry season; mean monthly maxima vary from 26.8 to 30.8°C and minima from 20.5 to 22.3°C (Tutin et al., 1997).

The geology of the park is dominated by old metamorphic and granitic bedrocks (Nicklès, 1952). In most of the study area, the altitude varies between 200 m and 300 m, with a few hills reaching 700 m.

Twenty forest types have been identified in the Lopé National Park, according to vegetation structure and composition (White, 1992). For the purpose of sampling, we distinguished the following habitats (White et al., 1995; White & Abernethy, 1997):

- Savanna: vegetation dominated by grass with scattered shrubs, mostly *Nauclea latifolia* and *Crossopteryx febrifuga* (Rubiaceae).
- Colonised savannas: adjacent to savannas, resulting from the colonisation of savannas by shrubs and pioneer trees such as *Aucoumea klaineana*, *Lophira alata* (Ochnaceae), and *Sacoglottis gabonensis* (Humiriaceae). As tree cover increases, colonised savannas turn into okoume forest.
- Okoume forest: monodominant *Aucoumea klaineana* forest. Canopy cover is discontinuous at 30–70%.
- Marantaceae forest: dominant tree species are *Aucoumea klaineana* and *Cola lizae* (Sterculiaceae), with other species belonging to the families Annonaceae, Ebenaceae,

Mimosaceae, and Myristicaceae relatively common. Canopy cover is discontinuous at about 85%, and the understorey is very dense, consisting primarily of herbaceous Marantaceae and Zingiberaceae.

- Mixed/Mature forest: higher tree species diversity, increased canopy cover (95%) and open understorey. Dominant tree families are Caesalpiniaceae, Olacaceae, Myristicaceae, Sapotaceae, Burseraceae, Irvingiaceae, and Euphorbiaceae.

These vegetation types form a dynamic succession from savanna to mature forest, each type being replaced by the next, to eventually reach the climax of mature forest (White, 2000).

In addition to this succession, other vegetation types were distinguished in our study:

- Rocky forest: associated with rock outcrops and thin soil. Trees rarely exceed 30 cm diameter at breast height; the canopy is 10–20 m high.
- Galleries: forest vegetation along streams and rivers (Ogooué) in savannas.
- Forest fragments: small patches of forest surrounded by savanna. They usually have an anthropogenic origin, being the remains of Iron Age villages (Oslisly & White, 1996). Typical tree families in forest fragments are Moraceae (figs), Arecaceae (palms), Bombacaceae, and Annonaceae.

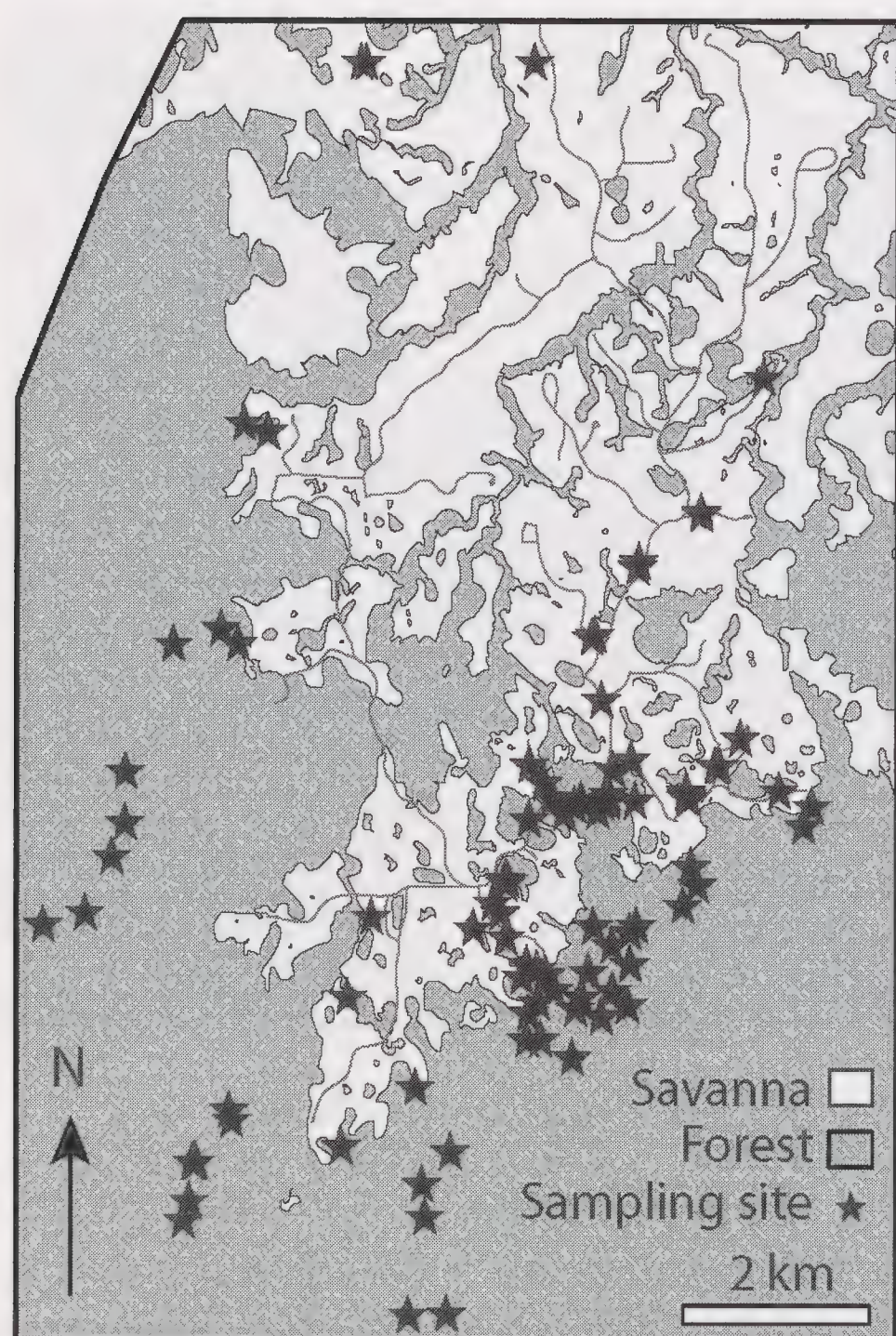


FIG. 2. Location of the sampling stations in the study area of SEGC (38 stations were outside the SEGC study area).

Two other habitats were sampled:

- Anthropogenic: In and around houses. However, we did not sample in plantations around Lopé, a village 15 km from our study site.
- River drifts: flood deposits along rivers. These do not represent a true habitat, because the empty shells they contain have been washed from upstream vegetation types that may be different from the one immediately surrounding the river drift. They were sampled for informative purpose only, but are not included hereafter.

Collecting Effort

Altogether, 132 stations were sampled. The core area surveyed (96 stations) covers approximately 50 km², corresponding to the study site of the Station d'Etude des Gorilles et des Chimpanzés (SEGC) (Fig. 2). We also collected outside the study site of SEGC (38 stations) in scattered places in the northeast of the park, mainly in the Mikongo area (14 sta-

tions) and along the Offoué River (eight stations). A station is defined as a collecting locality, spread over 5–10 m² at most, in a single habitat and microhabitat. When two microhabitats were sampled in the vicinity of each other, they were considered as two different stations; this approach differing from most other works (Tattersfield, 1996; De Winter & Gittenberger, 1998; Emberton et al., 1999) in which snails are usually searched for in all microhabitats in quadrats of a given area. This was intended to maximize the efficiency of sampling, focusing on microhabitats rather than habitats. The main microhabitats sampled, representing 89.1% of the stations, were leaf-litter in depressions on the ground (36.5%), leaf-litter between buttresses of large trees (26.3%), rotten logs (12.4%), leaf-litter at the base of trees without buttresses (8.8%), and rock crevices (5.1%). Other microhabitats included house walls, elephant bones, tree trunks, and bare ground. The distribution of stations across habitats and microhabitats is presented Table 1.

Sampling took place in three different periods: 30 August to 7 October 1999 (transition between dry and rainy seasons), 19 June to 11 August 2000 (dry season), and 21 April to 7 June 2001 (rainy season).

For each station, we recorded the geographical coordinates using a GPS GARMIN 12CX, as well as the habitat, microhabitat, exposure, altitude as given by the GPS and date.

At each station, two people spent 30 minutes searching at ground level for live snails, then leaf-litter and a few millimeters of topsoil were collected. This sample was processed at the collecting location with a Winkler sieve (1 cm mesh), the coarse material being checked for shells (empty shells and live animals) and discarded. The remaining material was bagged and sun-dried as soon as possible. The molluscs collected alive were drowned overnight and fixed in 70% ethanol for future dissection.

Once dried, the bagged leaf-litter material was weighed and its volume measured. Altogether, 445 liters of litter were collected. It was passed through 5 mm, 2 mm, and 0.6 mm sieves. The two larger fractions were thoroughly searched with the naked eye, the third one sorted under a dissecting microscope. Material passing through the 0.6 mm sieve was searched for the first three sites, but as it contained no molluscs, as was the case in earlier studies (e.g., Tattersfield, 1996; De Winter & Gittenberger, 1998), it was subsequently discarded.

TABLE 1. Number of stations per microhabitats and habitats.

	Rotten logs	Buttresses	Leaf- litter	Tree base	Tree trunk	Rock crevices	Bare ground	House wall	Elephant bones	Total
Mature	5	14	8	5		1				33
Marantaceae	7	8	8		1	1	3			28
Okoume	1	2	3			1				7
Rocky	2	3	7	1		1				14
F. fragments		8	7	3						18
Gallery	1	1	3	1						5
Col. Savannas	1		4							5
Savannas			6	2		3	1			12
Anthropic								4	1	5
River drifts			5							5

For seven stations, the dry material between 2 mm and 0.6 mm was separated into two equal parts. One was completely searched for molluscs, the other was poured into a bucket of water, and only the floating fraction (once re-dried) was searched for molluscs. As the number of shells found by flotation was not significantly different from that found by complete searching (Wilcoxon matched pairs test: $z = 1.57$, $N = 7$, ns), it was assumed that only a negligible number of shells were lost with this method, and the remaining samples were searched after floating, which improved efficiency. This method has been successfully tested by other authors (e.g., Cameron, 1986).

Twelve stations, in various vegetation types, were sampled twice, once during the rainy season (April–May) and once at the beginning of the dry season (end of June) to check for seasonal variability. These stations were marked with metal disks nailed to the trees to allow for their accurate relocation.

Taxonomic Processing and Data Analysis

All specimens were sorted to morpho-species, or Recognizable Taxonomic Units (New, 1999), by an experienced taxonomist (E.N.) according to shell characters, assigned to a family and, when possible, to a described genus or species. Few RTUs received specific identification. As we did not dissect animals, closely related species with similar shells may have been overlooked (in particular, urocyclid semi-slugs), so our diversity results could be underestimates. However, most of our RTUs are equivalent to species as generally understood by mollusc taxonomists, and in the Results and Discussion sections, “RTUs”

and “species” refer to the same concept. The genus and, to some extent, family allocations we have used are tentative, and many RTUs currently assigned to the same genus (or family) based on shell characters might belong to different genera (or families). In other words, our results are repeatable at species level, but should not be used to compare genus or family diversity in another country/continent.

In our analyses, we have combined animals collected alive and those collected dead, for two reasons: (a) we collected more dead shells than live animals, and did not want to exclude the bulk of our data from the analyses, and (b) it was sometimes difficult to determine whether shells had been collected alive or dead, because the material was processed by sun-drying, sometimes long after collection.

When possible, juvenile specimens were assigned to a RTU for which we had adult specimens. If more than one RTU matched with the juveniles (mostly urocyclids and some streptaxids), these juveniles were discarded from the diversity and abundance analysis. If the juvenile did not match any of the adult shells, it was treated as a separate RTU.

Heterogeneity between habitats and stations was measured with Whittaker’s index I , which is the total number of species recorded (S) divided by the mean number of species per station (Cameron, 1992; De Winter & Gittenberger, 1998). If I equals 1, all the stations have identical faunas, whereas higher values indicate increasing differentiation. Within-habitat evenness was measured by inverse Simpson’s index, which provides a good estimate of diversity at relatively small sample sizes and ranks assemblages consistently (Magurran, 2004). With inverse Simpson’s in-

dex, a higher diversity is reflected by a higher index.

Both height (H) and diameter (D) of the shell were measured from randomly selected adult specimens. As the global pattern of distribution of height and diameter classes is tightly linked to the choice of size classes (Allsopp, 1997; De Winter & Gittenberger, 1998; Bouchet et al., 2002), size classes were first represented with intervals equivalent to a 2-fold transformation. The X-axis was then logarithm (base 2) scaled to the size concerned. In order to get a better representation, we divided each class by 2, that is, using a 2-square-root-fold transformation.

In order to assess faunal assemblages, a Principal Components Analysis and a Cluster Analysis (euclidean distances, Ward’s method) were performed using Statistica 6.0 (StatSoft, Inc.).

The authority for the higher classification of Mollusca used in this study is Bouchet & Rocroi (2005).

Voucher material is deposited in the Muséum National d’Histoire Naturelle, Paris (France).

RESULTS

Species Richness

A total of 3,745 specimens representing 74 species were collected at the study site (Appendix). The fauna consists of 12 families (Fig. 3). Subulinidae were the most speciose family, with 26 species (ca. 35% of the total, and 62% of the total number of specimens), fol-

lowed by Streptaxidae (19 species, 26%) and Urocyclidae (12 species, 16%).

The species accumulation curve (Fig. 4) and the various richness estimators calculated via EstimateS 7.5 (Colwell, 2005) show that our sample represents between 56% (Chao2, 132 species) and 94% (Michaelis-Menton equation, 79 species) of the total extrapolated richness. EstimateS 7.5 provides 95% confidence intervals for Chao1 and Chao2 estimators, which are as follow: Chao1: 82.56–171.54; Chao2: 92.84–250.07.

Shell Size and Shape

The Appendix gives the height and diameter of 71 species collected – Veronicellidae (no shell) and semi-slugs (shells not identifiable to species) were not measured. Major shell dimension (either H or D, whichever is greater) ranged from 1.3 to 118.6 mm with a mean of 10.0 mm. As a result of the high number of small species compared to large ones, the median is only 5.5 mm and the mode is 3.5 mm. Figure 5 gives the distribution of the major shell dimension. Despite different size classes having been used by different authors, the size distribution in our study seems to follow the same pattern as others (Allsopp, 1997; De Winter & Gittenberger, 1998), even in a marine habitat (Bouchet et al., 2002), that is, a Poisson-like distribution with two main peaks, the first (smaller sizes) being higher than the second (larger sizes). Major shell dimension (H or D) of 30 species (42%) is less than 5 mm (37% in Cameroon, De Winter & Gittenberger, 1998); 42 species (59%) have a

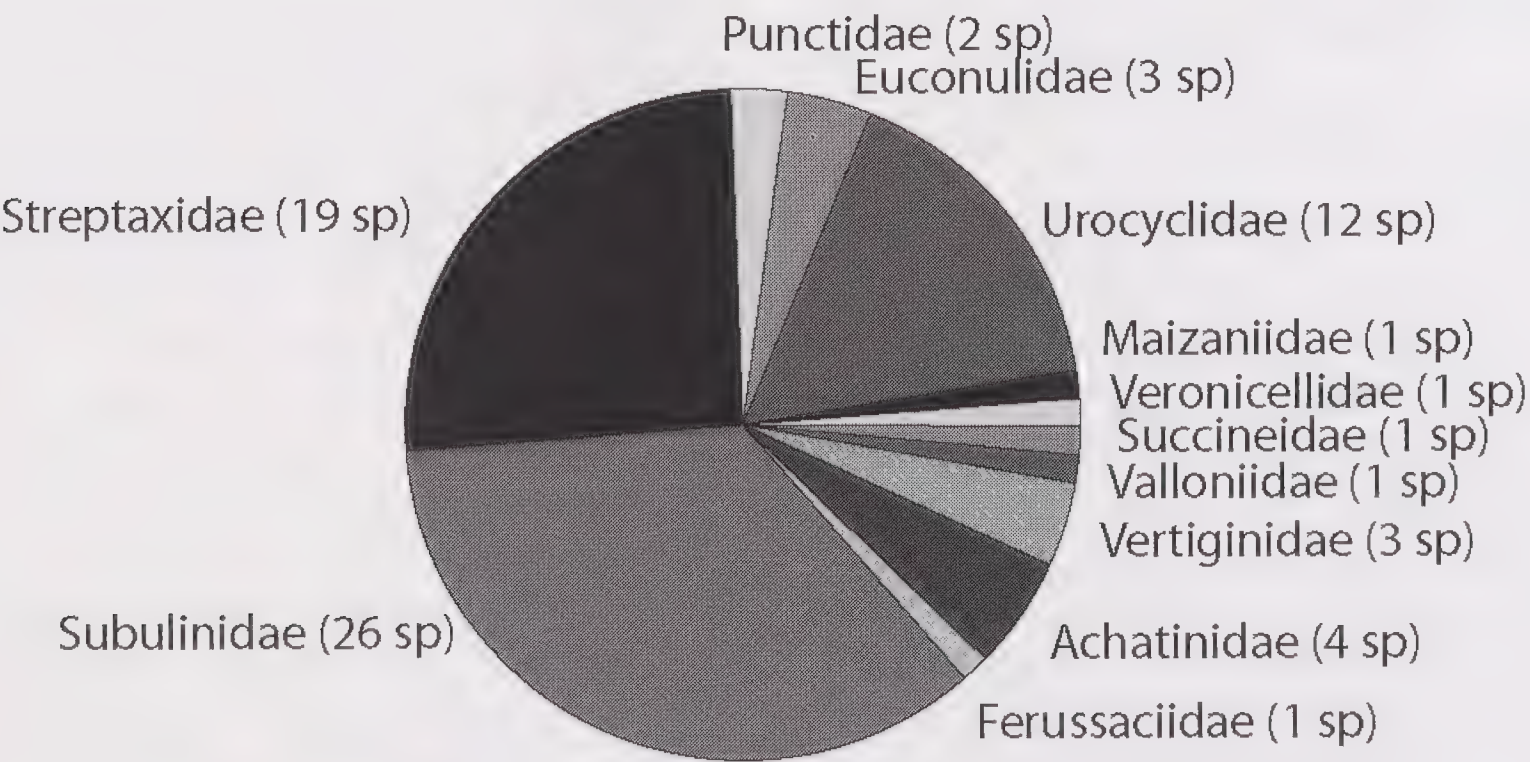


FIG. 3. Distribution of land snail families in Lopé National Park, Gabon.

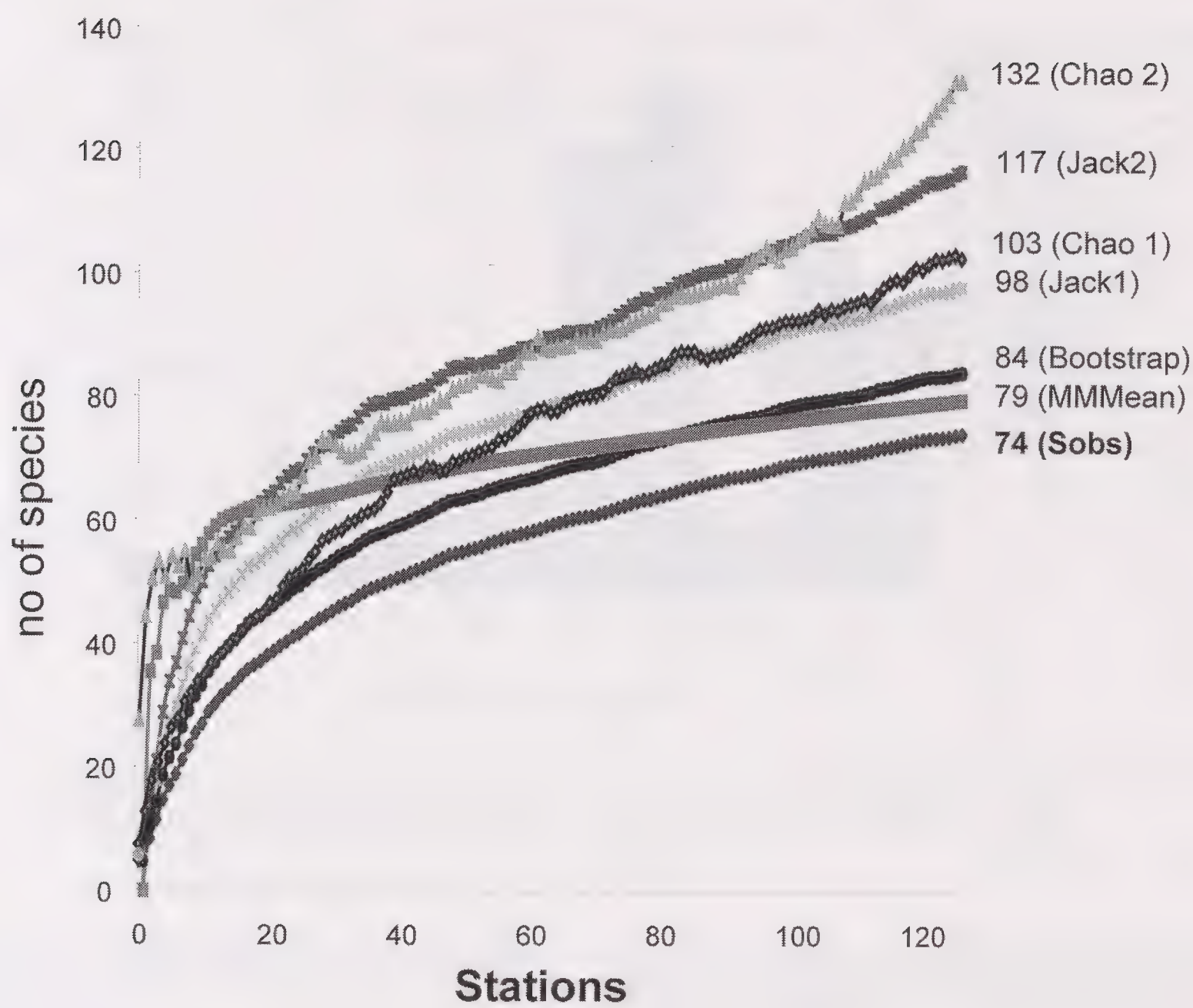


FIG. 4. Species accumulation curves based on EstimateS 7.5 (Colwell, 2005), with various richness estimators.

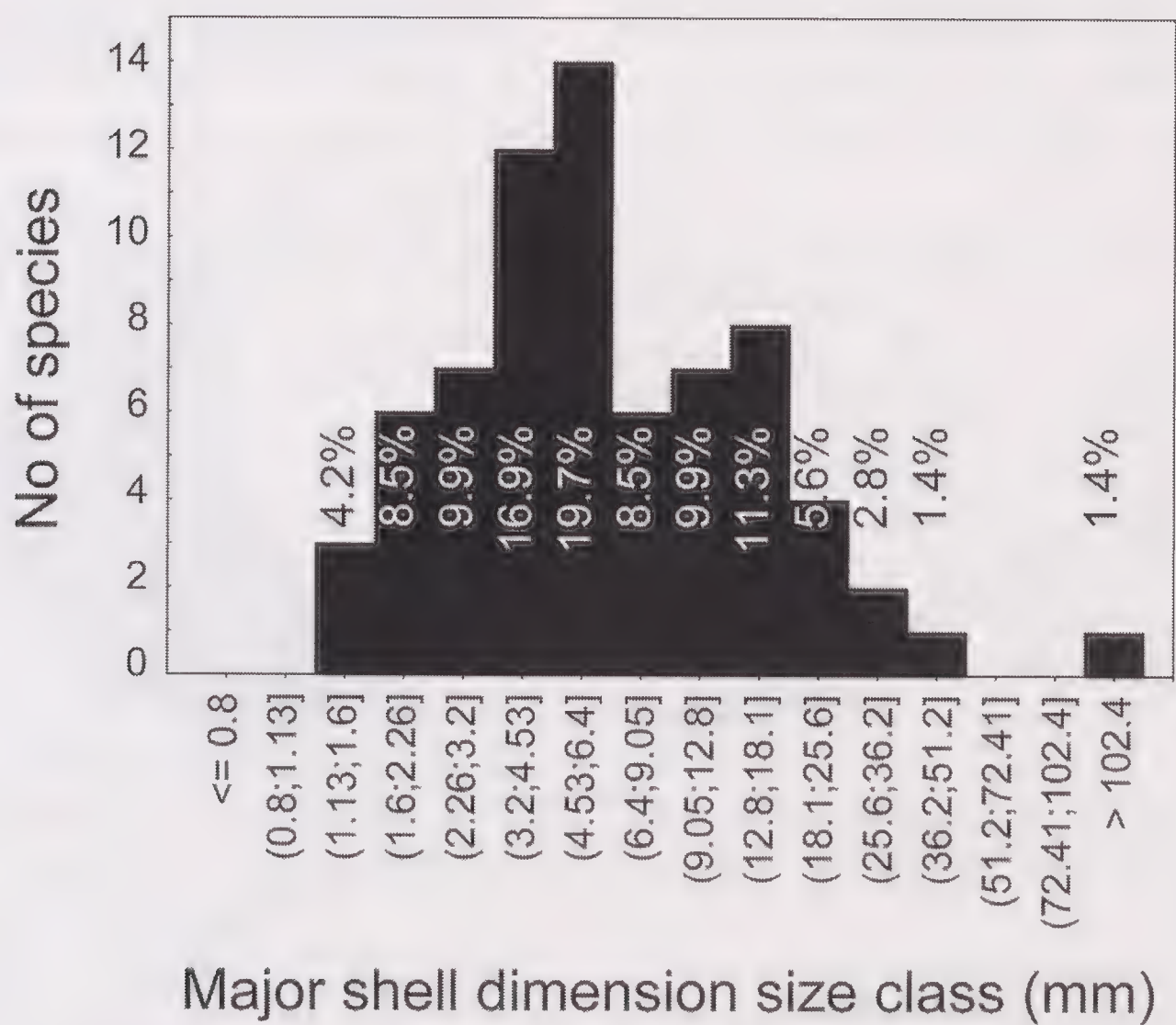


FIG. 5. Major shell dimension (height or diameter) distribution of 71 species living in the Lopé National Park, Gabon, based on randomly selected adult specimens. Size classes are intervals equivalent to a 2-square-root-fold transformation, or a 2-fold transformation for 2 classes.

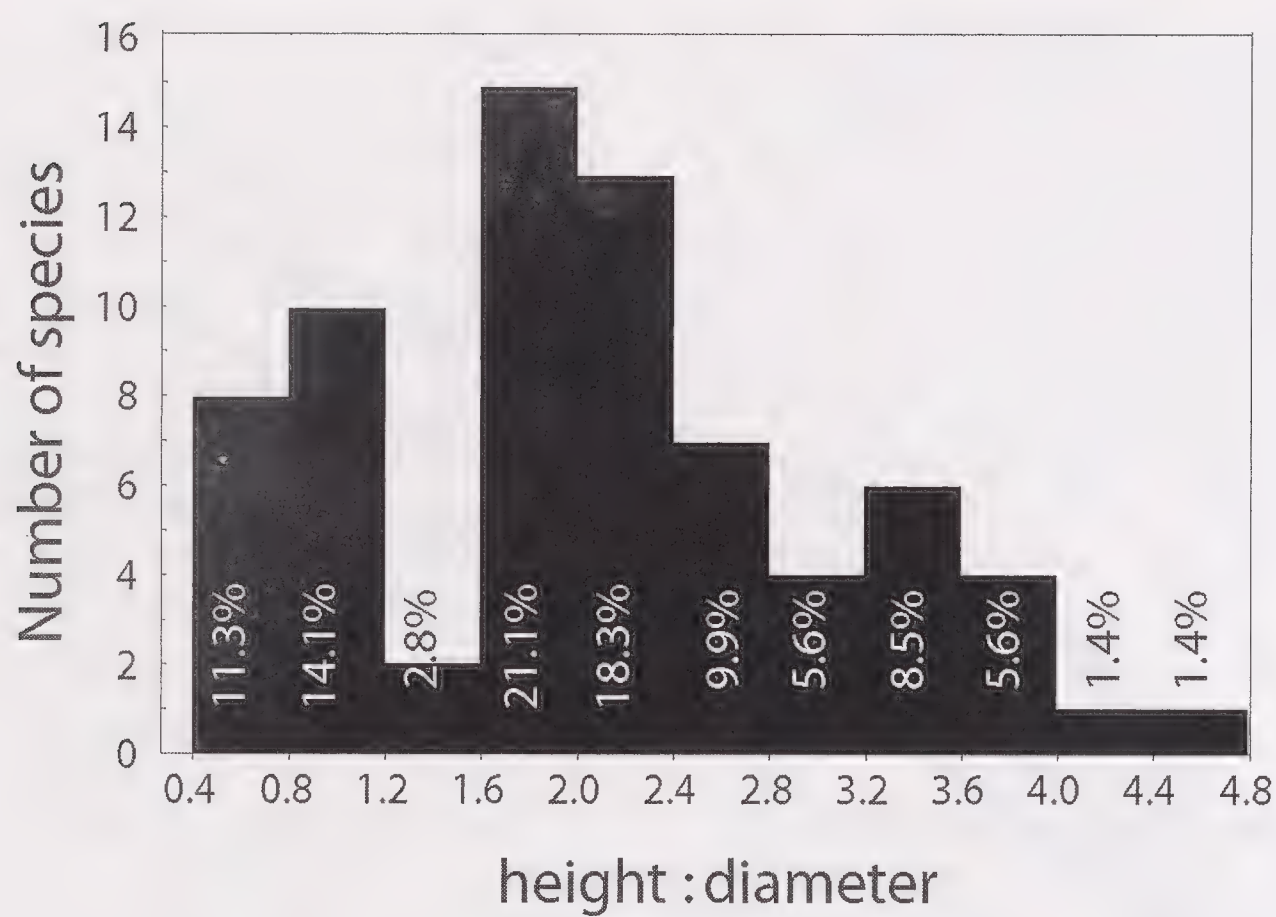


FIG. 6. Shell height:diameter ratio of 71 species living in the Lopé National Park, Gabon, based on randomly selected adult specimens.

major shell dimension less than 6.4 mm, and an additional 25 (35%) are between 6.4 and 25.6 mm.

Figure 6 shows a bimodal distribution of shell height:diameter ratio for the 71 species measured, with a high number of globose to flat species ($0.4 < H/D < 1.2$) and tall ($H/D > 1.6$) species. No species have $H/D < 0.4$ and very few have $H/D > 4.0$.

Rarity

Snail abundance is generally low in the study area. This can be expressed as biological rarity and ecological rarity, *sensu* Bouchet et al. (2002).

Biological Rarity – Biological rarity is estimated by the total number of specimens found of a given species. The dominant feature of

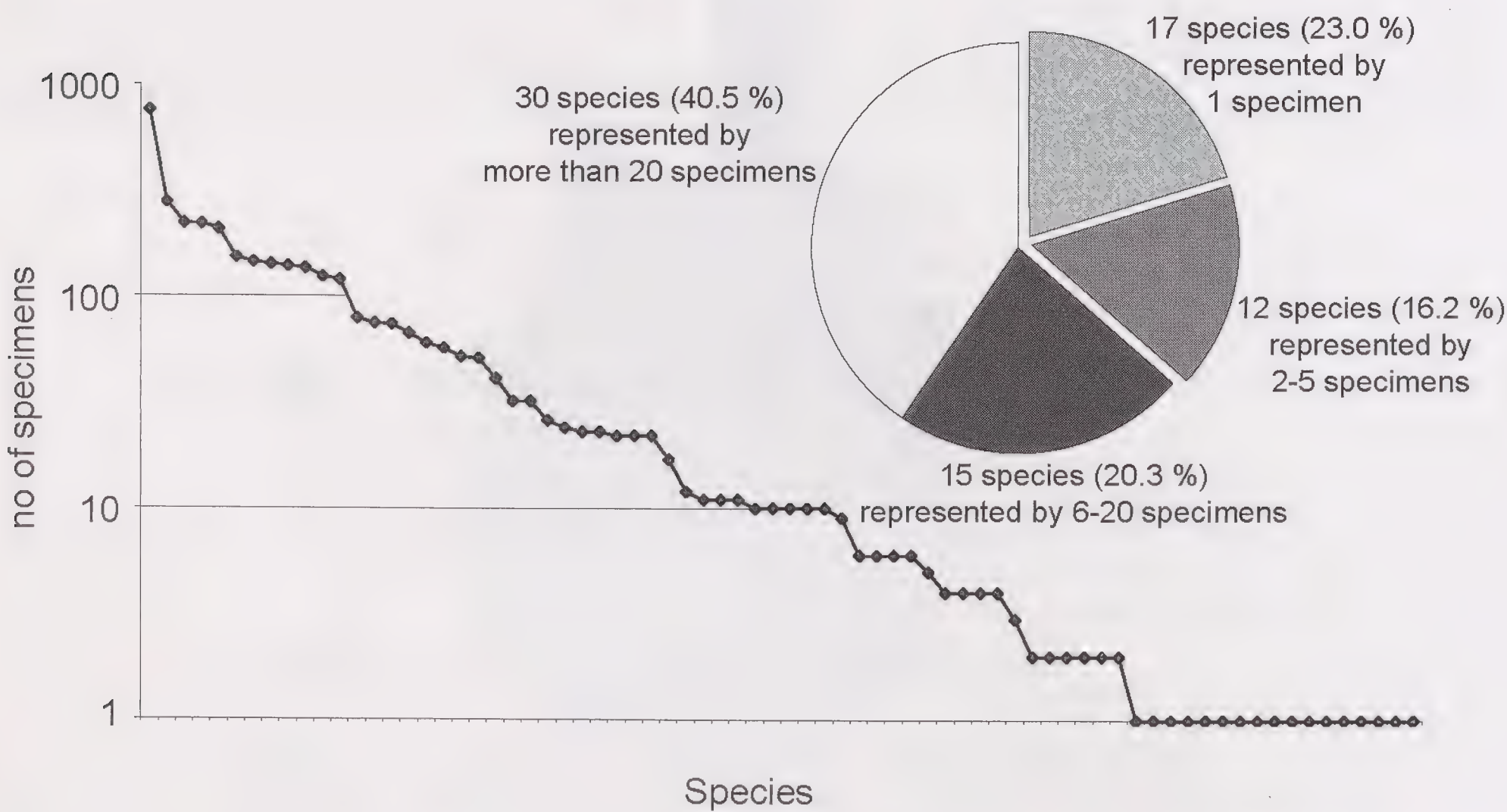


FIG. 7. Biological rarity of the terrestrial molluscs living in the Lopé National Park, Gabon. Proportion of species in four arbitrary abundance (number of specimens) categories and rank-abundance relationship.

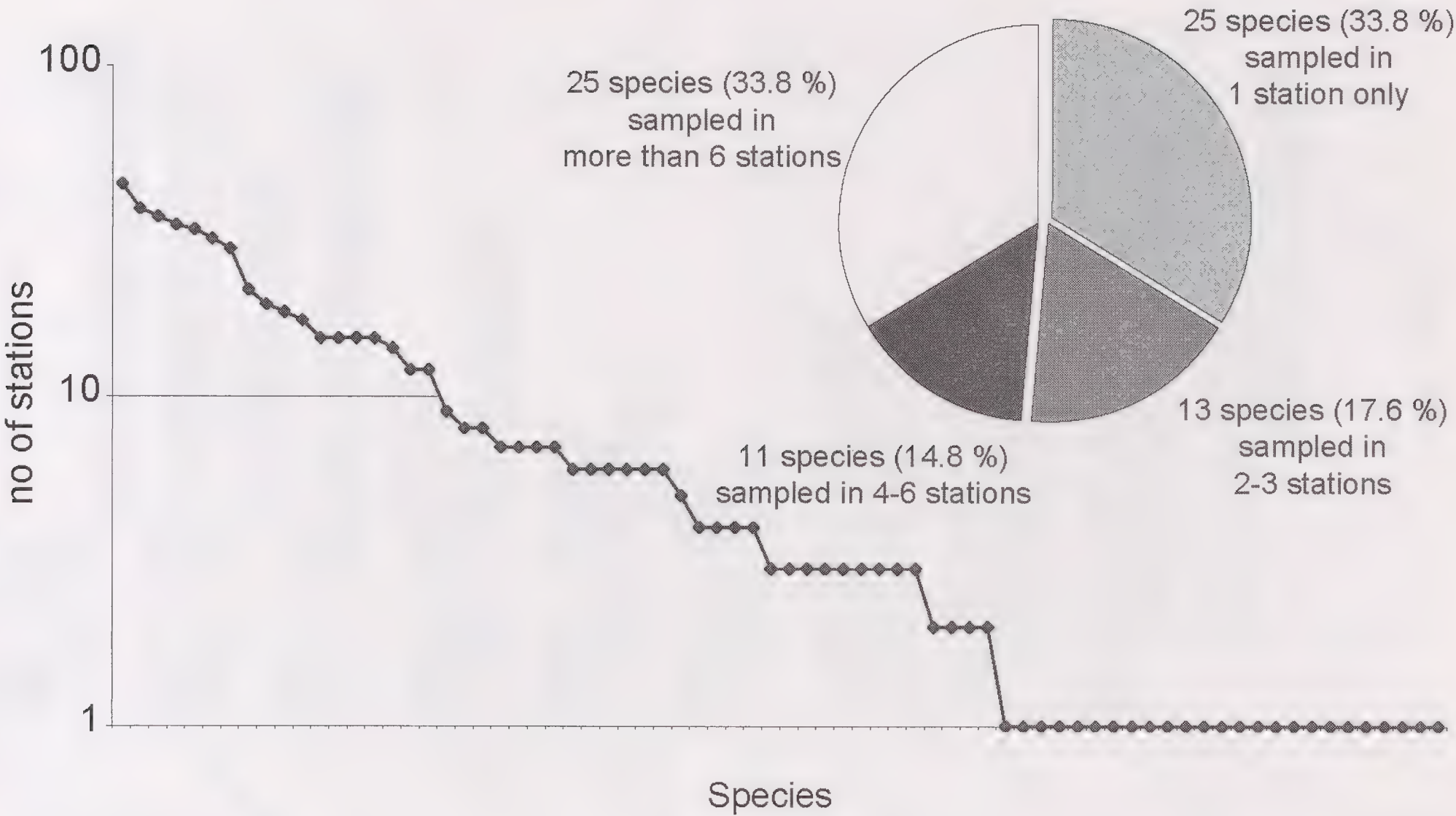


FIG. 8. Ecological rarity of the terrestrial molluscs living in the Lopé National Park, Gabon. Proportion of species in four arbitrary abundance (number of stations of occurrence) categories and rank-abundance relationship.

the fauna is the high frequency of rare species (Fig. 7). The average is 47.4 specimens per species, the median is 10 specimens per species, and the mode is one specimen per species.

A remarkable feature is the relative abundance of one species of Subulinidae, *Subulona decollata* (Morelet, 1873), with 804 specimens, that is, 21.5% of the total number of specimens. It was most abundant at one station (Gab159, in a forest fragment, with 602 specimens), where many individuals were associated with (perhaps feeding on) fallen flowers of *Ceiba pentandra*. Even if this station is discarded, *S. decollata* remains among the most abundant species.

When the quartile definition of rarity is followed (Gaston, 1994), 19 species fall into the category “rare”, with no more than two specimens. These species are represented by an average of 1.11 specimens. Among these 19 species, eight are Streptaxidae.

Ecological Rarity – Ecological rarity is estimated by the number of stations at which a species occurred. In Lopé, 25 species (33.8%) were only found at one station (including 11 Streptaxidae, five Subulinidae, four Urocyclidae). These necessarily include the 17 that are represented by only one specimen, plus eight others that are represented by more than

one specimen. Twenty-five species (33.8%) were found in more than six stations (Fig. 8). The average frequency of occurrence for the 74 species collected is 8.38 stations per species, the median is four stations per species and the mode is one station per species.

Species Richness and Abundance in Various Habitats

For the 74 species collected, Whittaker’s index was 14.0, which indicates a substantial degree of beta diversity. Table 2 gives Simpson’s index calculated for various habitats (more than ten sampling stations): according to this index, mature forest, rocky forest and Marantaceae forest are the most diverse habitats.

TABLE 2. Simpson’s Inverse Diversity Index for habitats covered by more than 10 stations.

Habitat	Simpson's Index
Mature forest	18.66
Rocky forest	15.19
Marantaceae forest	14.19
Forest fragments	4.54
Savanna	4.48

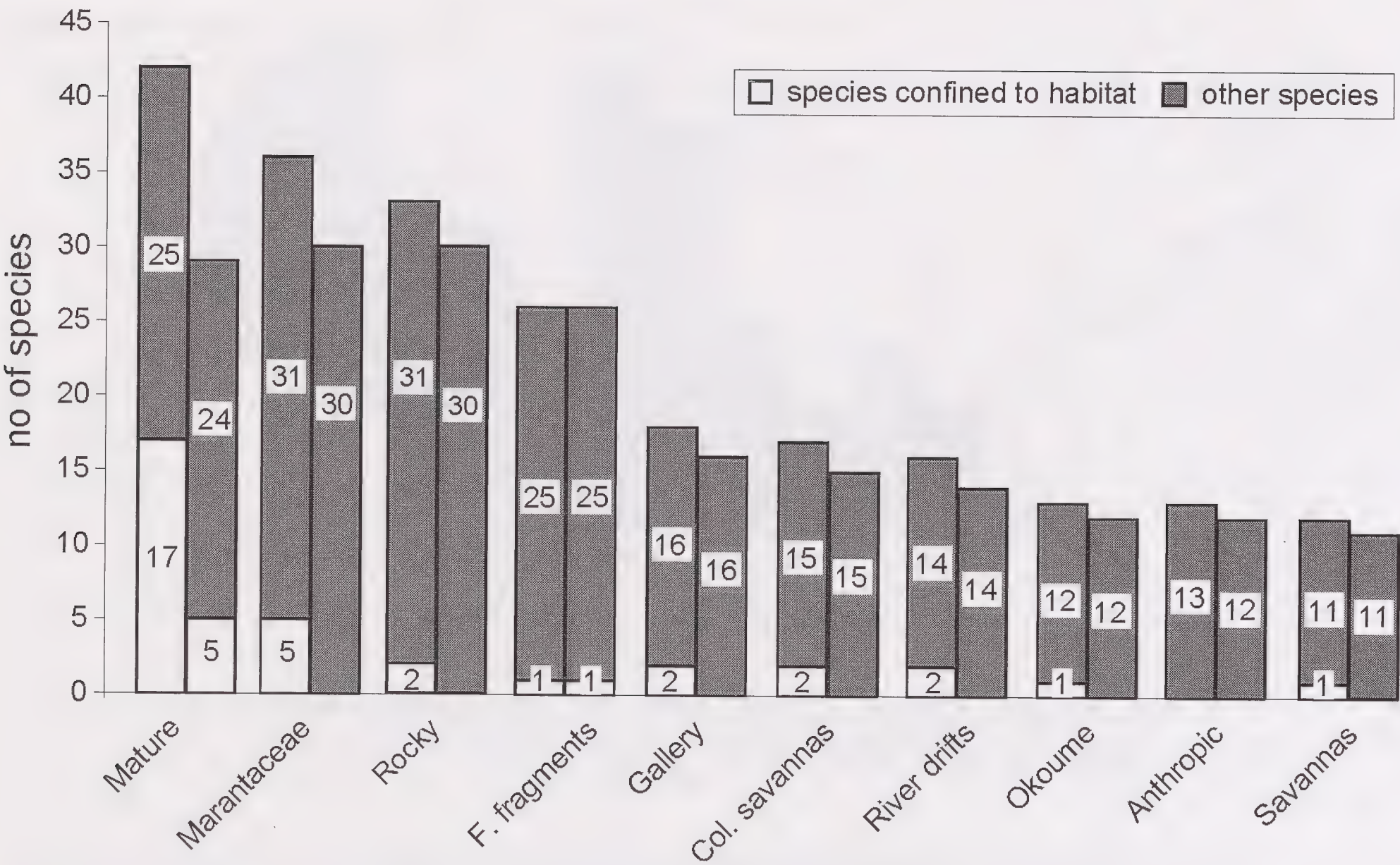


FIG. 9. Species diversity and ecological endemism in the various habitats of the Lopé National Park. For each vegetation type, the left bar include rare species (species present in more than two stations) whereas the right bar excludes them.

Four habitat types are much richer in species than the others (Fig. 9): mature forest, Marantaceae forest, rocky forest and forest fragments. Among these, mature forest has the highest species richness, as well as the highest number of species confined to a habitat: 57% of the fauna (42 species) occur in mature forest, and 23% of the total species are confined to this habitat. The other habitats have many fewer habitat-specific species. At the lower end, okoume forest, anthropogenic habitats and savannas are the least species-rich habitats. This is not linked to higher microhabitat diversity in mature forest: microhabitats as defined by us (between buttresses, leaf-litter in ground depressions etc.) were not more diversified in mature forest than in other forest types (Table 1). When rare species are excluded, this pattern does not change (Fig. 9). However, diversity in the various vegetation types is significantly correlated with sample size, measured by the volume of collected leaf-litter ($r = 0.88$, $p = 0.0015$): the more an habitat was sampled, the more species were collected.

There is some variation among the oldest forest types (i.e., mature and Marantaceae forest): we compared the fauna of these for-

ests in the SEGC study area (43 stations) and further south, in Mikongo and/or along the Offoué River (21 stations). A high proportion of the SEGC fauna was not found in Mikongo/Offoué (Fig. 10). However, despite the fact that there were twice as many stations in the SEGC than in Mikongo/Offoué, 14.0% (eight species) of the species found in mature and Marantaceae forests were only found in Mikongo and/or along the Offoué River. Species found in both areas are more abundant on average than species found in one area only, and are

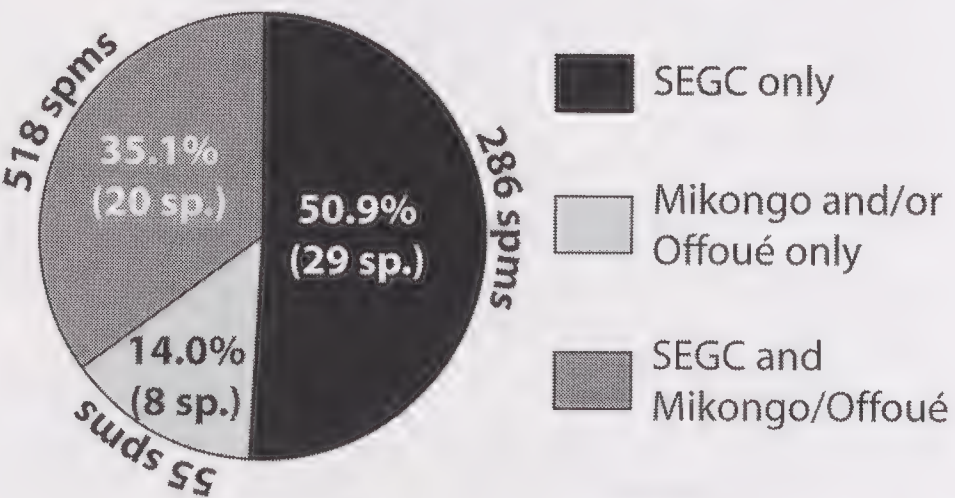


FIG. 10. Comparison of the fauna in mature forest and Marantaceae forest in SEGC study area and further south in the park (Mikongo and along the Offoué).

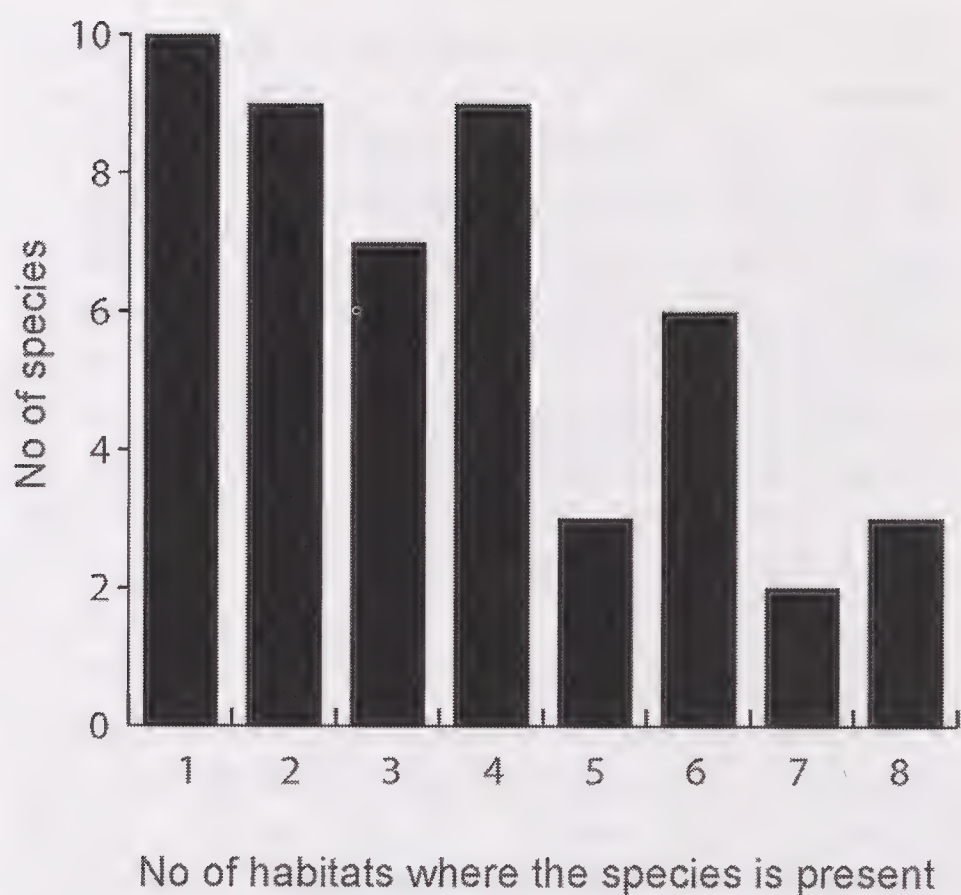


FIG. 11. Frequency distribution of the number of habitats for the 49 species found in more than one station. River drifts and anthropic habitats have been excluded.

thus easier to collect: that could account in part in the fact that they were found in both areas. However, species found in Mikongo/Offoué only were not necessarily rare: four were found in more than one station, and three had 10 specimens or more. This implies that even in superficially similar habitats, the fauna can change on a 15 km scale. In conclusion, the high beta diversity is the result of both habitat mosaic and geographical location.

Three species were found in all eight habitats (excluding anthropogenic habitat and river drifts) and two others in all but one habitat (Fig. 11). Among the 49 species present at more than one station, 10 were found in only one habitat (one species in galleries, one in forest fragments, one in rocky forest, and the remaining seven in mature forest). A few species seem to be highly habitat-specialized, a few others are ubiquitous, and most species are intermediate, dwelling in a number of forest habitats. Twelve species were found in savannas, and only one of these was not found anywhere else. It is a biologically rare species (only one specimen found), and it might be present in other habitats despite our not finding it anywhere else. The other savanna-dwelling species were also found in various habitats, from mature forest to colonised savannas. Altogether, only two species were confined to savannas and "close to savanna" habitats (forest fragments and galleries).

No molluscs were found at six stations (two in mature forest, two in savanna, one in rocky

forest and one in Marantaceae forest), and 13 stations produced only one species (five in mature forest, three in savanna, three in Marantaceae forest, and two in okoume forest). The two richest stations had 14 species each, and 12 stations had 10 or more species, in forest fragments, rocky forest, Marantaceae forest, mature forest, and anthropogenic habitat (respectively four, three, two, two and one station(s)).

The abundance of species (numbers of specimens) does not follow the same pattern as their diversity. Figure 12 shows that forest fragments constitute the richest habitat in term of abundance, even when the 602 specimens of *Subulona decollata* found on a single deviant station are discarded, followed by galleries and colonised savannas. Savannas and okoume forest are the least specimen-rich habitats, and the other forest types have an intermediate abundance of molluscs.

The six most abundant species in the study area belong to the Subulinidae (4 species), Urocyclidae (1 species), and Euconulidae (1 species). If station Gab159, where an extremely high number of *Subulona decollata* was found, is discarded, *Gudeella* sp. 2 (Urocyclidae) is the most abundant species.

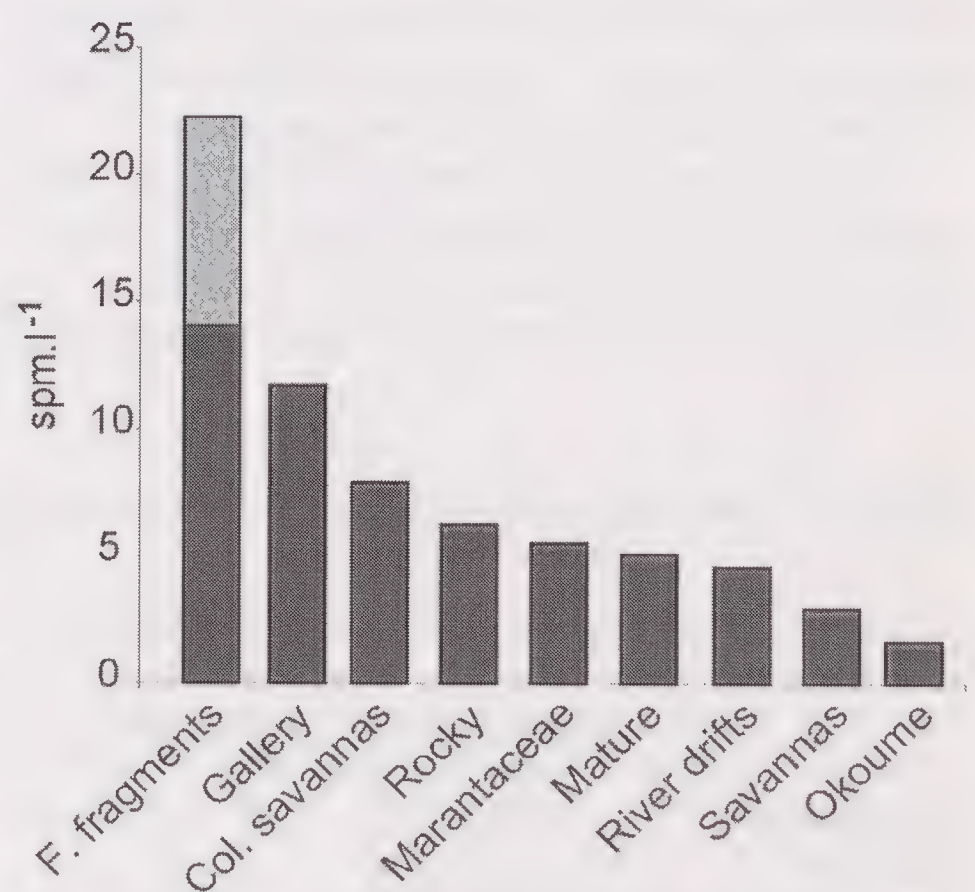


FIG. 12. Abundance of molluscs (number of specimens per volume of leaf-litter collected) in the various habitats of the Lopé National Park. The light grey area for forest fragments represents the 602 specimens of *Subulona decollata* found on station Gab159. Samples from anthropic habitat have been discarded since most of these were picked by hand, with no litter sieving. River drifts, although not representing a habitat, have been included for comparison.

Species Diversity in Microhabitats

The numbers of species found in each microhabitat are given in Table 3. Twenty-eight species (38%) were found in one microhabitat only, but 25 of these are rare species, found at only one station, and 36 species (48%) were found in three or more microhabitats. The species found at more than one station but always in the same microhabitat included two subulinids (*Ischnoglessula* sp. 1, three stations between buttresses, and *Striosubulina* sp. 4, three stations in leaf-litter) and a vertiginid (*Truncatellina* sp. 1, two stations between buttresses). Buttresses have the highest average number of species per station, though this is not significantly higher than for trees without buttresses (t-test, $t = 1.47$, $df = 45$, ns).

The rather unusual microhabitat of dry elephant bones yielded as many as 11 species (at one station): in this calcium-poor environment, bones probably represent an important source of calcium.

Seasonal Variation

Sampling took place during the rainy season and the long dry season. For the purpose of the seasonal variation analysis, sampling done in 1999 was discarded, because it occurred at the transition between dry and rainy season. The other sampling periods were well defined as occurring in one season only.

Sixty stations were sampled during the rainy season (267.2 L of litter collected) and 55 during the long dry season (119.8 L of litter collected). The total numbers of specimens were

2772 for the rainy season and 697 for the dry season, giving a mean number of specimens.L⁻¹ of 10.4 for the rainy season and 5.8 for the dry season. Neither the number of specimens.L⁻¹ nor the number of species.L⁻¹ differs significantly between seasons (Mann-Whitney U test, ns).

The total number of species was higher in the rainy season (60 species) than in the dry season (49 species), although not statistically significantly, and slightly fewer than half of the species (46%) were found in only one season: 22 species were found only during the rainy season, and 11 only during the dry season. However, if we discard rare species (only one or two stations where the species was found), for which no conclusion regarding seasonality can be drawn, their being so scarce, three species were only found during the rainy season, and two only during the dry season. Among the 38 species that were found in both seasons, there are more species that are more common during the rainy season than during the dry season (22 vs. 16); 22 species (58%) had a relative abundance (standardized per litter volume) differing by more than 50% between seasons.

A separate analysis was performed for the twelve sites sampled twice: the median number of species per site, standardized per litter volume, is significantly higher at the beginning of the dry season than during the rainy season (Wilcoxon matched pairs test: $z = 2.04$, $N = 13$, $p = 0.04$). However, the median number of specimens per site (standardized per litter volume) is not significantly different between the seasons (Wilcoxon matched pairs test: $z = 1.41$, $N = 13$, ns).

TABLE 3. Number of species and stations per microhabitat.

Microhabitat	Number of species	Number of stations	Average number of species/station	Average number of specimens/station
buttresses	50	36	6.6 ± 3.9	42.5 ± 50.8
leaf-litter	47	50	4.3 ± 2.6	18.5 ± 17.8
base of trees without buttresses	34	12	4.8 ± 3.1	23.8 ± 20.9
rotten logs	27	17	3.7 ± 2.6	9.8 ± 15.25
rock crevices	22	7	3.7 ± 3.1	14.0 ± 20.9
elephant bones	11	1		
house walls	6	4	2.3 ± 1.5	2.3 ± 2.3
tree trunks	1	1		
bare ground	1	4		

Faunal Assemblages

In order to estimate if snail faunal assemblages match vegetation types (White et al., 1995), we performed a Principal Components Analysis with a matrix of species within stations. However, no obvious pattern was evident, the abundance and ecological rarity of species being the main factors generating the clustering, even when rare species were removed.

A cluster analysis of a presence/absence matrix of species within stations did not produce any obvious pattern either. The main factor determining clustering was the number of species within stations. Among the species-poor stations, all the mature forest stations above 400 m asl were clustered together, with other mature forest stations from lower areas. Geographical proximity was not a factor determining clustering (stations from Mikongo are spread all over the dendrogram), neither was the type of microhabitat. However, the clus-

tering distances was low, and the faunal partitioning did not seem to be determined by the vegetation types seen by botanists.

DISCUSSION

Habitat Diversity

No work has been published in a scientific journal on the plant richness in the various forest types in the Lopé National Park. White (1992) had some data, but these are now completely outdated because new inventories have been made (White, pers. comm.). However, White et al. (1995) quote the fact that older forest types are richer than younger ones, and scientists working in Lopé confirm this fact (White, pers. comm.; Tutin, pers. comm.). Not surprisingly, mollusc species richness seems to follow plant species richness (Fig. 9), the richest habitats for snails being the most bo-

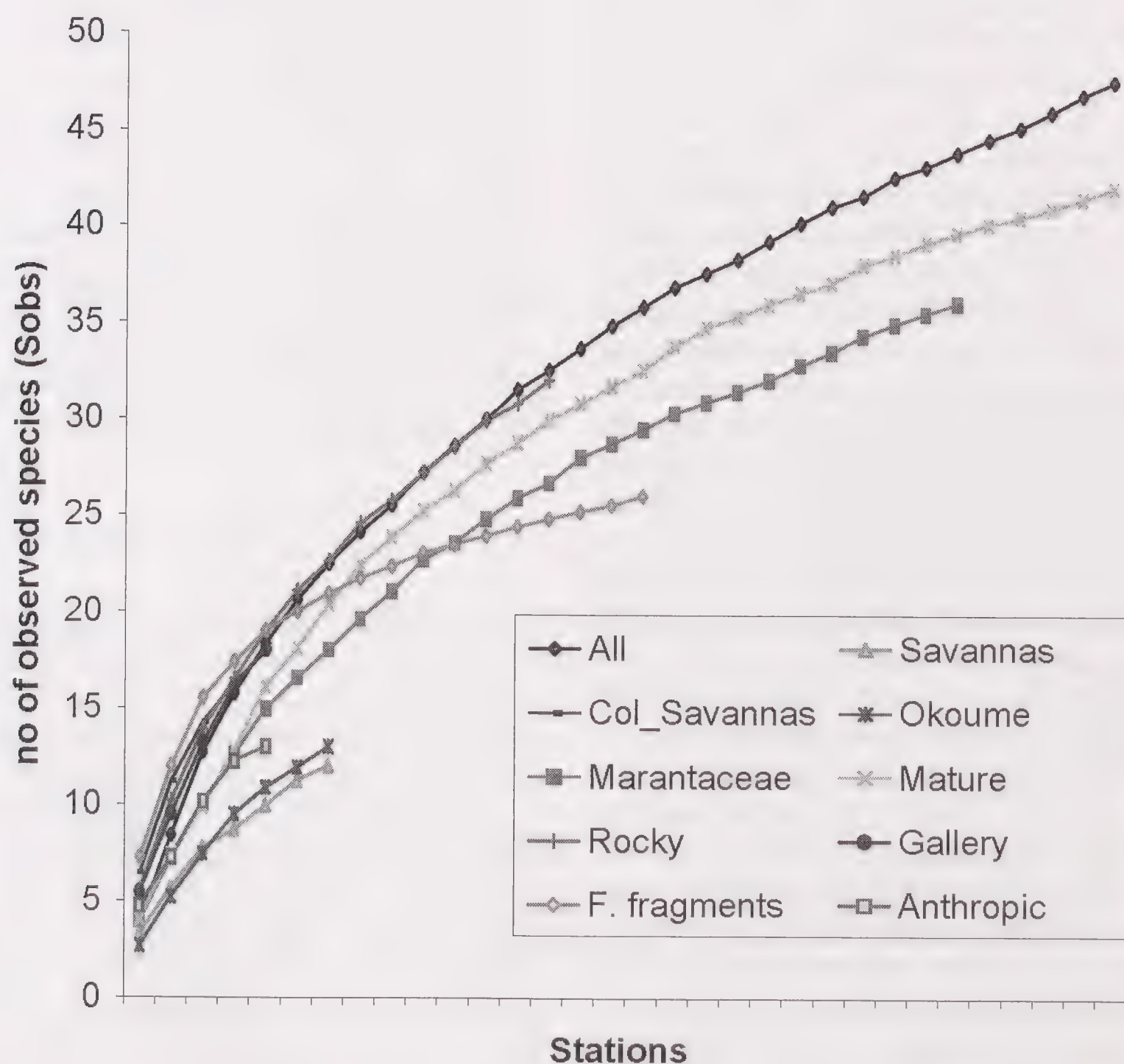


FIG. 13. Species accumulation curves for various habitats based on EstimateS 7.5 (Colwell, 2005). River drift sites have been discarded, not representing a true habitat.

tanically diverse vegetation types, that is, mature and Marantaceae forest, which are at the end of the succession from savannas to old forests, and rocky forest and forest fragments, which are out of this succession but are old vegetation types. Rocky forest is a very rich habitat for molluscs, as shown by Simpson's index (Table 2); even with a lower collecting intensity than in forest fragments, it is more diverse. As we defined microhabitats, our analyses do not show an association of species and microhabitats, and as they are similarly distributed in the various forest types, they cannot account alone for the variation in our data. If microhabitats had been more finely defined (e.g., pH, substratum, humidity, exposure), it might have been possible to examine whether they can explain species distribution. This was not the case in our sampling protocol, so it is safer to discuss species diversity and associations at the habitat level, be it determined by microhabitats, precise floral composition or other factors.

However, the ranking of vegetation types is biased by the fact that the various vegetation types were not sampled with the same intensity (Table 1). For example, galleries and colonised savannas seem to be poorer than other vegetation types, but they also had a lower collecting effort (fewer stations were prospected there than in mature or Marantaceae forests). Indeed, diversity in the various vegetation type is significantly correlated with sample size (measured by number of stations or volume of collected leaf-litter). To account for this bias, a species accumulation curve was constructed for each habitat (Fig. 13). As most of these curves do not show any evidence of flattening, a measure of the confidence of the richness estimates is given Figure 14. Mature forest has the highest number of species, followed by Marantaceae forest, rocky forest, and forest fragments. However, for rocky forest, a larger number of sampled stations would have permitted confirmation of this tendency. Okoume forest and savannas are the poorest habitats, falling well below the other curves. This is not surprising: savanna is a harsh habitat, dry and sunny, with almost no organic soil and few sheltering microhabitats; okoume forest is much more homogeneous than the other forest types, and the low diversity of other organisms, including plants, might well be reflected in the low diversity of molluscs. Nevertheless, these two habitats, as well as galleries, colonised savannas and anthropo-

genic habitats were not sampled enough to draw definite conclusions from these curves. From these results, it is however clear that the savannas in Lopé do not have a specific fauna: except for one rare species (*Pseudopeas* sp. 3), no species was restricted to savannas. The savannas in Lopé are isolated in a sea of forest, the closest savannas being 200 km away, and are subject to frequent fires (usually every second or third year). Most species in savannas also live in other forest types, and probably recolonize the savannas from the forest after burning episodes. On a larger scale (the whole of southern Africa), Bruggen (1978) drew similar conclusions, that is, southern African savanna-dwelling land molluscs are de-

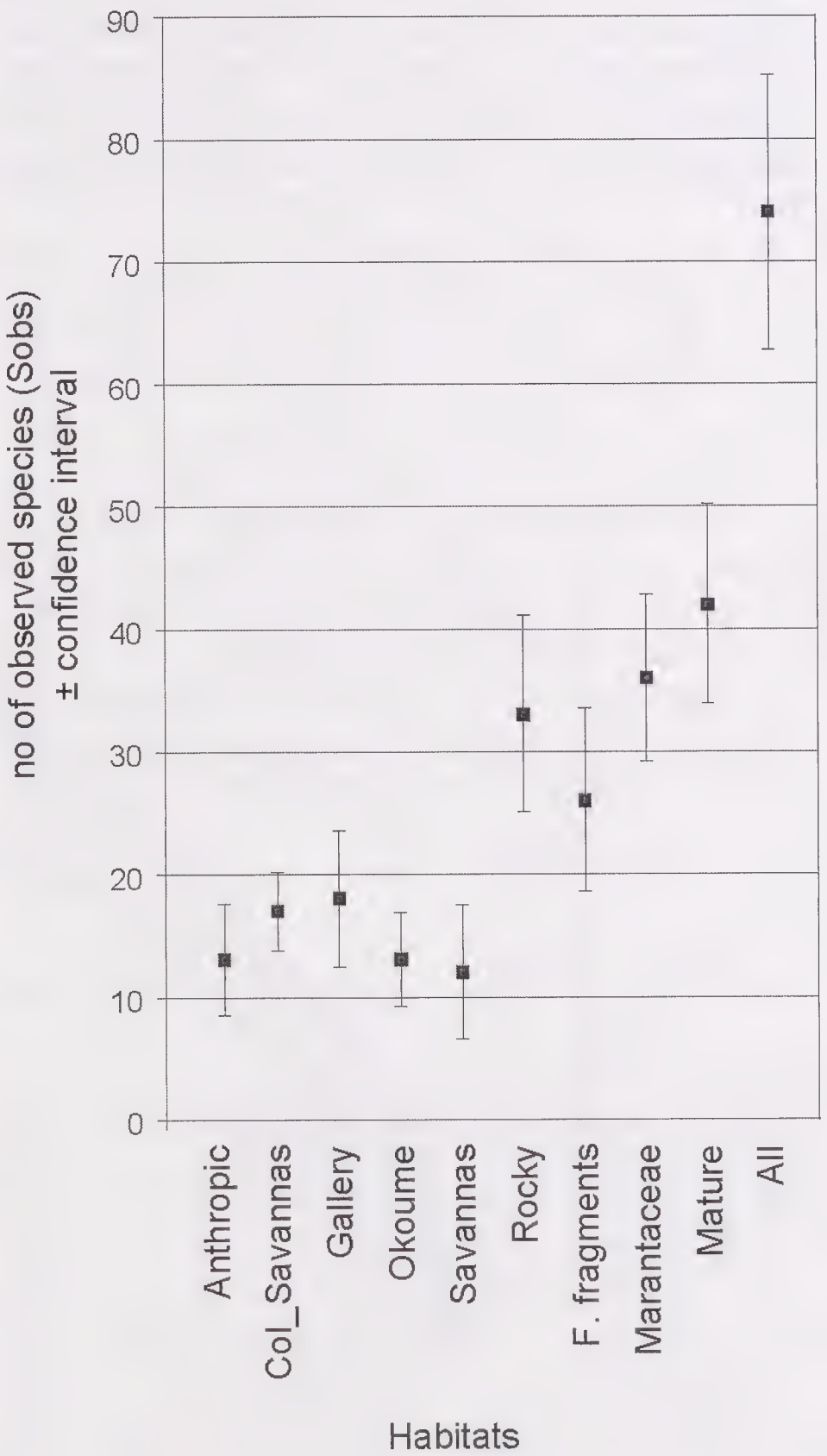


FIG. 14. Number of species expected in the pooled samples for various habitats with 95% confidence intervals, based on EstimateS 7.5 (Colwell, 2005). Habitats are ranked according to the increasing number of stations.

rived from, or are ecologically widely tolerant, forest taxa.

There is also some variability within habitats, as shown by the comparison between the mature and Marantaceae forests of the SEGC study area and the Mikongo/Offoué area. Simpson's index for mature forest in Lopé is 18.66, which is high, but might be influenced by the sampling not being exhaustive, with many biologically or ecologically rare species.

Striosubulina sp. 7 is among the most abundant species in forest fragments, galleries and savannas, and, except for one station in Marantaceae forest, less than 100 m from the forest edge, has not been found in other habitats (particularly forest). This species is commonly found in plantations, gardens and urban areas all over Gabon (BF, pers. obs.): it is probable that in Lopé, it has followed the human population in ancient settlements (destroyed a long time ago and now turned into forest fragments) and has spread in the open habitats around them. On the other hand, *Gudeella* sp. 2, which is also one of the most abundant species in forest fragments, galleries, colonised savannas and savannas, has also been found at several stations in Marantaceae forest, mature forest, and rocky forest (three, seven and four stations respectively): it is a generalist, living in all the habitats from open savanna to dense mature forest. However, the possibility that *Gudeella* sp. 2 is in fact a complex of closely related species should not be excluded, its shell having few characteristic features and no anatomical studies having been performed.

Seasonal Variation

Our data show no significant difference in either abundance or diversity of land snails between the rainy and dry seasons. Indeed, the so-called "dry" season has the same level of atmospheric humidity as the rainy season (Tutin & Fernandez, 1993). There is dew in the morning all year long, and land snails probably do not suffer from a shortage of water in the "dry" season: for the period 1984–2002, on average, 10.4% (154.8 mm) of the annual rainfall occurred during the long dry season (SEGC, unpublished data). However, some species seem to be more abundant during one part of the year, probably because of such behaviour as aestivation/hibernation (animals are more concealed part of the year), or because they have a life cycle of one year or

less. The fact that in the twice-sampled sites, the number of species is significantly higher at the beginning of the dry season than during the rainy season also suggests that there could be seasonality in the life cycle of some species. However, we cannot rule out the fact that results from the sites sampled twice could be influenced by disturbance, or recolonisation factors following the first sampling. The paucity of data regarding life history of land snails in tropical Africa prevents any firm conclusions on seasonality, but similar results have been found in other studies (De Winter & Gittenberger, 1998).

The results regarding seasonality are biased by the fact that sieving the leaf-litter produces many dead individuals (empty shells), which are not necessarily representative of the fauna at a given time of the year. Seasonality would be better studied with live individuals only, but as was indicated in the Methods section, it is difficult and time-consuming to sort out animals collected alive from those collected dead, especially for minute species.

Shell Size and Shape

The distribution of H/D is very similar to that presented by De Winter & Gittenberger (1998), but very different from that for the faunas of sites in Madagascar, New Zealand, and USA (Emberton, 1995), which are all unimodal with a peak in the 0.4–0.8 class (flat shells). Our fauna includes a large proportion of globose shells, mainly Urocyclids (*Teleozonites* spp. and *Trochozonites* spp.). However, more than 70% of our species are tall (H/D > 1.0), reflecting the abundance of Streptaxidae and particularly Subulinidae. This abundance of tall species contrasts with the faunas presented by Emberton (1995). Cain (1977) suggested that on average, high-spined species would favour vertical surfaces (trees, rocks), whereas low-spined species would tend to live on the ground. In Lopé, where we did not find truly arboreal species, a high proportion of the ground-foraging species are high-spined, contrary to Cain's hypothesis.

The range of shell size in Lopé is huge, from 1.3 mm to 118.6 mm, but most species are small to minute. The proportion of minute species (*sensu* Emberton, 1995), shell diameter 0–5 mm) is even higher than in the Cameroon site (De Winter & Gittenberger, 1998) or the Madagascar site (Emberton, 1995) (74% vs. 66% and 63% respectively), but the overall

pattern of size distribution is the same, with very few large species. Together with the rarity of many species, this emphasizes the fact that mollusc sampling cannot be done with the naked eye only, and should be done with litter sieving, the fastest way to collect minute species in significant numbers.

Streptaxids as Predators

As reviewed by De Winter & Gittenberger (1998), carnivorous streptaxids are a prominent part of the malacofauna of the Afrotropical region, representing between 18% (Tattersfield, 1996) and 46% (Emberton et al., 1997) of the fauna. Lopé is no exception to this situation, with streptaxids representing 26% of the species found, but as much as 38% of the biologically rare species and 34% of the ecologically rare species. On the other hand, subulinids, which represent 35% of the species, constitute only 20% of the biologically rare species and 26% of the ecologically rare species; urocyclids, which represent 16% of the species, constitute 17% of the biologically rare species and 18% of the ecologically rare species. When the number of specimens is considered, streptaxids constitute 8% of the total number of specimens, subulinids 63% and urocyclids 14%. The relative rarity of streptaxids compared to subulinids and urocyclids might be linked to their feeding ecology, streptaxids being carnivorous whereas subulinids and urocyclids are phytophagous, but data supporting this speculation are lacking. However, a single streptaxid species – *Streptostele musaecola* (Morelet, 1860) – is both abundant (126 specimens found) and widely distributed, in various habitats (28 stations, seven habitats). *Streptostele musaecola* was described from Africa (Morelet, 1860), but is known to be an invading species, with a circumtropical distribution (Solem, 1988b; Hausdorf & Medina Bermudez, 2003), and is probably highly adaptable.

Richness and Diversity

In its overall composition, the malacofauna of Lopé resembles that of rainforest in southwestern Cameroon (De Winter & Gittenberger, 1998) and in another part of Gabon (De Winter, 1995), the most speciose families being Subulinidae, Streptaxidae, and Urocyclidae. However, streptaxids are the most speciose family in Cameroon, whereas subulinids are the most speciose family in Lopé.

The Lopé malacofauna comprises at least 74 species in approximately 50 km², and up to 132 species according to the Chao2 richness estimator (Fig. 4). These figures are in the same order of magnitude as results of other studies in tropical Africa. The richest site known to date in a tropical environment is in Cameroon, with 97 species (and up to 108 according to the richness estimators) in 1 km² of rainforest (De Winter & Gittenberger, 1998). This high diversity is further emphasised by the fact that “only” 2,654 specimens were collected at the Cameroon site, compared to 3,745 in our study, and that there was only one type of macro-habitat in the Cameroon site, that is, very old secondary forest. In 265 km² of indigenous forest and secondary vegetation in Kenya, Tattersfield (1996) found 53 species, and estimated that there should be 70–80 species in total. In the rainforest of two mountain ranges of southeastern Madagascar, Emberton et al. (1999) reported 80 species, though they did not pretend to have made a complete inventory. The only other study in Gabon (De Winter, 1995) listed 32 species in 48 km² of rainforest, but they were collected by a “malacologically inexperienced botanist” during floristic transects, so this inventory is probably far from complete. In tropical America, Gargominy & Ripken (1998) found 32 species in 1 km² of rainforest. On a smaller scale, Rosenberg & Muratov (1998) found 73 species of terrestrial molluscs in 4 ha in Jamaica; this diversity is probably linked to the site being in a karst area, where molluscan diversity and abundance are always high. In Cameroon, De Winter & Gittenberger (1998) found 83 species on 9 ha of rainforest, a huge diversity for acidic soils.

At the Cameroon site, 27 species (28% of all species) were found only on understorey vegetation, at 75 cm or more above the ground. In a study using the same methodology (beating of understorey vegetation) in Sabah (Schilthuizen & Rutjes, 2001), 11% (7 species) of the fauna was strictly arboreal. Our collecting method did not involve systematic beating of understorey vegetation, but we never found snails on the leaves of understorey plants, and very rarely on tree trunks. Whether this lack of arboreal fauna represents a sampling bias or is real, it accounts at least in part for the lower richness of Lopé compared to Cameroon.

Another reason for this lower richness could lie in the vegetation history. The area we stud-

ied, in the northern part of the Lopé National Park at the edge of the savanna, is mostly composed of “young” forest, resulting from the extensive recolonisation of savannas that occurred between 1500 and 700 years BP, when humans left the area and fires were rare (Oslisly & White, 1996; White, 2000). Unlike the Cameroon example, the forest of the northern part of the Lopé National Park is not a Pleistocene forest refuge (Maley, 1996), which might be related to the lower number of species found in Lopé compared to the Cameroon site. This could also account for the fact that arboreal snails are less abundant in Lopé than in the Cameroon site, as these are the most likely to be dependent on long periods of uninterrupted humid forest cover, and would have disappeared when the forest was replaced by savannas. On the other hand, the diversity of habitats and the presence of ecotones probably account for the fact that Lopé still ranks among the richest sites. However, outside the tropics, restricted areas in Australia, New Zealand, and the Carpathians mountains can also have a fauna of more than 70 species (R. Cameron, comm. pers.).

Sampling Problems

The value of our Whittaker's index is very high compared to other similar studies (compiled in Cameron & Pokryszko, 2005). However, the average number of specimens per station is lower than the total number of species collected during this survey: it is not possible for all species to be recorded at each station. Thus, sampling errors (i.e., the failure to find a species in a station) most probably account for this high value, together with habitat heterogeneity. Moreover, species richness in various habitats is significantly correlated with the amount of collected leaf-litter (i.e., with sampling intensity), as is the case in other studies (Cameron & Pokryszko, 2005). This is a further indication that sampling was not exhaustive, because if all species had been collected, more sampling would not add more species. Implications of sampling differences between habitats have been discussed above, but they are difficult to avoid if the aim is to perform an exhaustive inventory: in the field, one checks in priority habitats that should yield the best results, and poorer habitats are given less attention.

Towards an Ideal Strategy for a Maximum Efficiency of Tropical Forest Molluscan Biodiversity Inventories

All the studies cited above use a combination of direct search and litter sieving (except De Winter, 1995), which allows the most efficient inventorying, as was stressed by several authors (Emberton et al., 1996; Cameron & Pokryszko, 2005). The amount of time spent searching on the spot varied according to the available manpower, usually between one and three person-hours. Not everybody can afford 66 people collecting during a whole day, totaling 450+ person-hours (Emberton, 1995)! The volume of litter collected varied between 4 L and 8 L per station in the various studies.

Molluscs are not uniformly distributed in the forest: our sampling shows that some areas are devoid of molluscs, whereas others, in the same macrohabitat, exhibit high richness and abundance. The importance of the microhabitat cannot be underestimated, and can lead to sampling biases. Random sampling would have led to a much lower number of specimens being found, as is suggested by (1) the paucity of specimens from our (few) randomly located sampling sites, and (2) the variability of the number of species found in three stations less than 15 m away from each other (between the buttresses of a *Ceiba pentandra*, 12 species; between the buttresses of an okoume, nine species; in a depression on the floor, four species). Other studies have shown that random quadrats alone are not an efficient method for inventory (Cameron & Pokryszko, 2005). On a meso scale, our sampling was random (choice of the general area in a given habitat), but the microhabitats (between buttresses, under logs, in depressions) were carefully chosen.

The importance of carefully choosing the sampling spots is emphasized by the results of the other study in Gabon (De Winter, 1995), where the choice of the stations was random (following floristic transects), and not aided by a malacologically experienced eye. The diversity of the fauna found during this study was low, compared to our own or the Cameroon one, given that the habitat is a central African undisturbed lowland rain forest in all three studies. It seems certain that careful collecting done by an experienced collector would add many species.

In a given area, the choice of the habitat sampled is also important. Old undisturbed vegetation types should be given priority, for they usually harbour a higher diversity in tropical environments: the richest sites known to date are in these types of habitats (this study; De Winter & Gittenberger, 1998; Emberton et al., 1999; Schilthuizen & Rutjes, 2001). Other habitats should also be sampled, and may yield species that are restricted to them. But if the aim is to maximise the inventory, rather than to perform an ecological comparison, old undisturbed vegetation types should be sampled with a higher intensity than other habitats.

The inventory of a given area should not be extrapolated to the surrounding region. As shown by the differences of fauna between Mikongo and the SEGC area in our study, apparently homogeneous habitat can harbour different faunas at a 15 km scale. This result is comparable to that found in Cameroon: in three similar sites (30 km apart at the most), 32% of the malacofauna was present in only one of the sites (De Winter, 2001). Similar results have been found in coral reefs (Bouchet et al., 2002). In this respect, to achieve the most exhaustive inventory for an area, sampling should not only cover the various habitats, but also be spread over the entire area to account for geographical variation.

Last but not least, considering the generally high proportion of ecologically rare and small species, it is necessary to collect a lot of litter. For Europe, 20 l of leaf litter are considered adequate to sample the fauna of oligotrophic sites (Cameron & Pokryszko, 2005), it is probably a minimum for sites such as Lopé. The sorting is time-consuming, but flotation is an efficient way of reducing the amount of material to be sorted.

Limits of the RTU Approach

The main purpose of the RTU (morpho-species) approach is to circumvent the taxonomic impediment. In most cases, a classical approach, with full taxonomic identifications, could never be done in a reasonable amount of time, because of the lack of expertise and funding. This new way of dealing with tropical faunas and the use of proper collecting techniques are responsible for the complete shift of opinions regarding molluscan biodiversity in tropical forests. The studies cited above, which have changed our vision compared to

that of Solem (1984), that is, generally low diversity of land snails in rain forests, were published with a high proportion of species unidentified.

The use of RTUs in biodiversity studies has been criticized (Slotow & Hamer, 2000; Krell, 2004), mainly because morphospecies sorting is usually done by "parataxonomists", who do not have good knowledge of the specific taxonomic characters of the study group. Their results are not always reliable, often lead to overestimation of the number of species and the accuracy can be very low. However, our approach has avoided those problems because the sorting has been done by an experienced mollusc taxonomist (E.N.), who has followed the usual steps of taxonomic processing of samples, but stopped the process before giving names to RTUs. The samples have been placed in an accessible collection, namely that of the Muséum National d'Histoire Naturelle, Paris.

However, the RTU approach has some drawbacks:

- The RTUs have significance only for the people who have created them: a list of RTUs is useless to anyone else (only the number of RTUs can be used by others). This approach does not allow comparisons of the composition of faunas studied by different authors. The range of an RTU outside the study area cannot be known, and in particular, it is not possible to work on endemism, as the literature cannot be used to know whether a given RTU occurs somewhere else. This point is important from a conservation perspective. As was highlighted by Slotow & Hamer (2000), the number of RTUs in a given area is of little help for conservation planning, as these can be widespread and common species.
- If the study highlights some concerns about the conservation of a given RTU, it is impossible to take legal measures at the species level: to be listed in a Red List or a protected species list, a species has to have a recognised name. In the case of invertebrates, it is often more efficient to work at the habitat level than at the taxon level; however, the importance of Red Lists or protected species lists should not be underestimated. Names are a key to get access to scarce resources such as funds and expertise.
- When RTUs are used, it is impossible to know what proportion of a fauna remains to be

described. In some groups, this proportion can be huge (up to 80%, for instance in Bouchet et al., 2002).

In order to be able to validate the significance of RTUs, voucher material must be placed in an appropriate accessible collection (New, 1999).

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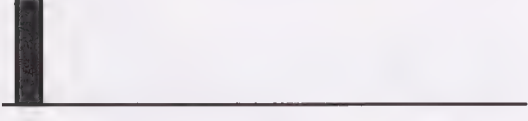
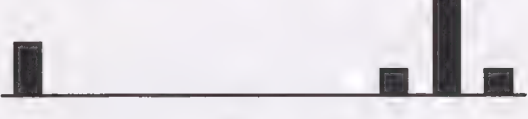
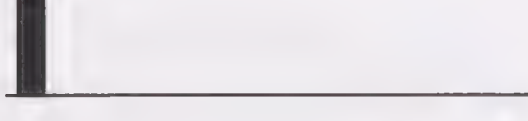
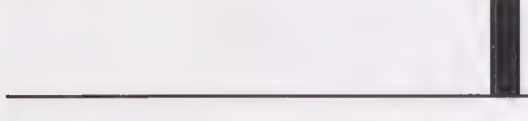
APPENDIX

List of land snail taxa recorded in the present study with total numbers of collected specimens, total number of stations where the taxon was found, shell morphometrics (height, diameter, and height-diameter ratio, all measured from randomly selected adult specimens). Right-hand column: bars indicate for each species the proportion of stations in each habitat type.

Taxon	Family	Total specimens	Total stations	Height (mm)	Diameter (mm)	H/D	MATURE MARANTACEAE OKOUME COL_SAVANNAS SAVANNAS ROCKY FOREST_FRAGM RIVER_DRIFTS ANTHROPIC GALLERY
<i>Maizaniella (Spiruloziana) lilliputiana</i> (Morelet, 1873)	Maizaniidae	67	6	2.2	3.4	0.65	
Veronicellidae spp.	Veronicellidae	17	12	-	-	-	
<i>Quickia</i> sp. 1	Succineidae	26	3	5.4	3.8	1.42	
<i>Pupisoma</i> sp. 1	Valloniidae	2	1	1.7	1.5	1.13	
<i>Truncatellina</i> sp. 1	Vertiginidae	6	2	1.6	0.8	2.00	
<i>Nesopupa</i> sp. 1	Nesopupidae	1	1	1.3	0.7	1.86	
<i>Nesopupa</i> sp. 2	Nesopupidae	1	1	1.4	0.8	1.75	
Subulinidae ? sp. 1	Subulinidae	10	5	3.7	1.2	3.08	
<i>Pseudopeas</i> sp. 1	Subulinidae	208	37	5.9	2.4	2.46	
<i>Pseudopeas</i> sp. 1a	Subulinidae	75	17	5.4	2.5	2.16	
<i>Pseudopeas</i> sp. 2	Subulinidae	120	35	4.2	1.7	2.47	
<i>Pseudopeas</i> sp. 3	Subulinidae	1	1	3.1	1.3	2.38	

(continues)

(continued)

Taxon	Family	Total specimens	Total stations	Height (mm)	Diameter (mm)	H/D	MATURE MARANTACEAE OKOUME COL_SAVANNAS SAVANNAS ROCKY FOREST_FRAGM RIVER_DRIFTS ANTHROPIC GALLERY
<i>Pseudopeas</i> sp. 4	Subulinidae	41	9	4.1	2.2	1.86	
<i>Pseudopeas</i> ? sp. 5	Subulinidae	22	7	3.2	1.2	2.67	
<i>Curvella</i> sp. 1	Subulinidae	10	4	5.1	2.4	2.12	
<i>Curvella</i> sp. 2	Subulinidae	11	6	5.4	2.2	2.45	
<i>Striosubulina</i> sp. 1	Subulinidae	6	3	12.2	3.8	3.21	
<i>Striosubulina</i> sp. 2	Subulinidae	142	6	15.4	3.7	4.16	
<i>Striosubulina</i> sp. 3	Subulinidae	4	3	17.2	4.8	3.58	
<i>Striosubulina</i> sp. 4	Subulinidae	23	3	18.6	5.8	3.21	
<i>Striosubulina</i> sp. 5	Subulinidae	52	6	15.1	4.1	3.68	
<i>Striosubulina</i> sp. 6	Subulinidae	221	14	16.4	4.33	3.73	
<i>Nothapalus</i> ? sp.	Subulinidae	1	1	14.8	5.4	2.74	
<i>Dictyoglessula</i> sp. 1	Subulinidae	6	3	8.2	4.3	1.91	
<i>Oleata</i> ? sp. 1	Subulinidae	2	1	15	4.7	3.19	
<i>Oleata</i> ? sp. 3	Subulinidae	4	1	10.3	4.6	2.24	

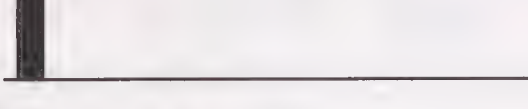
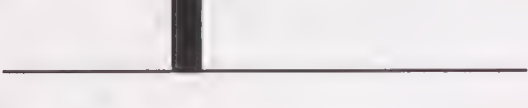
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Taxon	Family	Total specimens	Total stations	Height (mm)	Diameter (mm)	H/D	MATURE MARANTACEAE OKOUME COL_SAVANNAS SAVANNAS ROCKY FOREST_FRAGM RIVER_DRIFTS ANTHROPIC GALLERY
<i>Ischnoglessula</i> sp. 1	Subulinidae	32	3	8.8	2.8	3.14	
<i>Ischnoglessula</i> sp. 3	Subulinidae	22	7	10	2.9	3.45	
<i>Subulona</i> sp. 1	Subulinidae	139	21	10.8	2.4	4.50	
<i>Subulona decollata</i> (Morelet, 1873)	Subulinidae	759	19	23.2	6.6	3.52	
<i>Pileata</i> sp. 1	Subulinidae	136	32	17.6	6	2.93	
<i>Pileata</i> sp. 2	Subulinidae	2	1	20.4	5.5	3.71	
<i>Kempioconcha</i> sp. 1	Subulinidae	220	8	9.8	4.8	2.04	
<i>Cecilioides</i> sp. 1	Ferussaciidae	11	6	1.9	0.7	2.71	
<i>Achatinidae</i> gen. sp. 1	Achatinidae	2	2	36.1	18.3	1.97	
<i>Achatina balteata</i> Reeve, 1849	Achatinidae	1	1	118.6	62.2	1.91	
<i>Leptocala mollicella</i>	Achatinidae	5	4	24.7	14.7	1.68	
<i>Limicolaria</i> sp. 2	Achatinidae	24	7	41.1	18.4	2.23	
<i>Streptaxidae</i> sp. 1	Streptaxidae	6	2	2	3.5	0.57	
<i>Edentulina</i> sp.	Streptaxidae	1	1	5.9	4.6	1.28	

(continues)

(continued)

Taxon	Family	Total specimens	Total stations	Height (mm)	Diameter (mm)	H/D	MATURE MARANTACEAE OKOUME COL_SAVANNAS SAVANNAS ROCKY FOREST_FRAGM RIVER_DRIFTS ANTHROPIC GALLERY
<i>Streptostele</i> sp. 3	Streptaxidae	79	18	13.1	3.6	3.64	
<i>Streptostele (Tomostele) musaecola</i> (Morelet, 1860)	Streptaxidae	124	30	5.9	1.7	3.47	
<i>Varicostele</i> sp. 3	Streptaxidae	10	4	6.2	2.6	2.38	
<i>Gulella</i> s. lat. sp. 2	Streptaxidae	1	1	8.5	4.4	1.93	
<i>Gulella (Avakubia)</i> sp. 1	Streptaxidae	1	1	4.5	1.9	2.37	
<i>Gulella (Avakubia)</i> sp. 2	Streptaxidae	2	1	3.1	1.6	1.94	
<i>Gulella (Paucidentina)</i> sp. 1	Streptaxidae	11	2	2.9	1.5	1.93	
<i>Gulella (Paucidentina)</i> sp. 2	Streptaxidae	22	12	4	1.7	2.35	
<i>Gulella (Paucidentina)</i> cf. <i>monodon</i> (Morelet, 1873)	Streptaxidae	9	6	8.4	3.9	2.15	
<i>Gulella (Paucidentina)</i> sp. 4	Streptaxidae	1	1	3.0	2.9	1.03	
<i>Parennea (Parennea)</i> sp. 4	Streptaxidae	1	1	2.7	1.3	2.08	
<i>Ptychotrema (Ennea)</i> sp. 3	Streptaxidae	1	1	5.1	2.3	2.22	
<i>Ptychotrema (Ennea)</i> sp. 4	Streptaxidae	23	8	3.5	1.8	1.94	

(continues)

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Taxon	Family	Total specimens	Total stations	Height (mm)	Diameter (mm)	H/D	MATURE MARANTACEAE OKOUME COL_SAVANNAS SAVANNAS ROCKY FOREST_FRAGM RIVER_DRIFTS ANTHROPIC GALLERY
<i>Ptychotrema (Ennea)</i> sp. 5	Streptaxidae	1	1	3.5	1.6	2.18	
<i>Ptychotrema (Ennea)</i> sp. 6	Streptaxidae	4	1	3.0	1.7	1.76	
<i>Ptychotrema (Ennea)</i> cf. <i>sylvatica</i> Pilsbry, 1919	Streptaxidae	1	1	3.2	1.3	2.46	
<i>Marconia</i> sp. 1	Streptaxidae	2	1	9.7	5.5	1.76	
<i>Afropunctum</i> cf. <i>seminium</i> (Morelet, 1873)	Punctidae	60	15	1	1.6	0.63	
<i>Afropunctum</i> sp. 2	Punctidae	10	4	1.3	2.1	0.62	
<i>Kaliella</i> cf. <i>barrakporensis</i> (L. Pfeiffer, 1852)	Euconulidae	145	33	2.8	2.9	0.97	
<i>Afroguppya</i> sp. 1	Euconulidae	1	1	1.7	1.9	0.89	
<i>Afroguppya</i> sp. 2	Euconulidae	153	28	0.8	1.4	0.57	
<i>Trochozonites</i> cf. <i>bifilaris</i> (Dohrn, 1878)	Urocyclidae	1	1	4	3.9	1.03	
<i>Trochozonites</i> sp. 4	Urocyclidae	10	3	4.6	4.2	1.10	
<i>Trochozonites</i> sp. 6	Urocyclidae	74	15	5.5	5.4	1.02	
<i>Trochozonites</i> sp. 8	Urocyclidae	12	1	7.0	7.4	0.95	

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Taxon	Family	Total specimens	Total stations	Height (mm)	Diameter (mm)	H/D	MATURE MARANTACEAE OKOUME COL_SAVANNAS SAVANNAS ROCKY FOREST_FRAGM RIVER_DRIFTS ANTHROPIC GALLERY
<i>Teleozonites adansoniae</i> (Morelet, 1848)	Urocyclidae	51	15	5.5	5.4	1.02	
<i>Teleozonites</i> sp. 2	Urocyclidae	1	1	4.5	4.7	0.96	
<i>Thapsia</i> sp. 3	Urocyclidae	1	1	5.9	9.6	0.61	
<i>Thapsia</i> cf. <i>trogodytes</i> (Morelet, 1848)	Urocyclidae	3	3	26	15	1.73	
<i>Gudeella</i> sp. 1	Urocyclidae	57	7	3.6	6.0	0.60	
<i>Gudeella</i> sp. 2	Urocyclidae	279	44	4.5	8.1	0.56	
<i>Zonitarion</i> (<i>Belonarion</i>) n. sp. 1?	Gymnarionidae	4	3	-	-	-	
<i>Zonitarion</i> (<i>Belonarion</i>) n. sp. 2?	Gymnarionidae	32	15	-	-	-	